CONTRIBUTIONS TO PALAEONTOLOGY

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# STUDIES ON THE FOSSIL FLORA AND FAUNA OF THE WESTERN UNITED STATES.



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# A COMPARATIVE STUDY OF THE BRIDGE CREEK FLORA AND THE MODERN REDWOOD FOREST.

By RALPH W. CHANEY.

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# A COMPARATIVE STUDY OF THE BRIDGE CREEK FLORA AND THE MODERN REDWOOD FOREST.

By Ralph W. Chaney.

## INTRODUCTION.

There is an increasing amount of evidence to indicate a close relationship between certain of the Tertiary floras of the western United States and groups of plants now living in the same general region. Too often the emphasis of correlation in palaeontologic studies tends to result in a disproportionate consideration of the differences between fossil and living groups, and their resemblances pass unnoticed. This paper is written with the purpose of pointing out the similarity between the fossil Bridge Creek flora and the living redwood forest. The Bridge Creek flora is found in the Tertiary of the John Day Basin and other parts of Oregon; the redwood forest is limited to the Coast Ranges of California. Once established, such a similarity makes possible the interpretation of the living conditions of the Bridge Creek epoch in terms of the modern forest.

Studies in the Great Basin during the past four years have been carried on with the assistance and advice of Dr. John C. Merriam, and for the past two years with his cooperation as president of the Carnegie Institution of Washington. From Dr. Frank H. Knowlton the writer has received assistance of greatest value in connection with the study of Tertiary floras. In the study of modern floras many valuable suggestions have been made by Dr. Frederic E. Clements and Dr. Harvey M. Hall of the Carnegie Institution of Washington, by Dr. Willis L. Jepson of the University of California, and by Dr. LeRoy Abrams of Stanford University. Dr. Clements has been of especial assistance in the formulating of the principles of palaeoecology.

## GEOLOGIC OCCURRENCE OF THE BRIDGE CREEK FLORA.

The importance of the John Day Basin in the working out of the Tertiary history of the Great Basin is due to the relatively complete section there exposed, and to the association of abundant vertebrate and plant fossils at several horizons. Although visited by geologists and collectors for more than fifty years, the stratigraphy of the region was incompletely known until 1901 when Merriam published his Contribution to the Geology of the John Day Basin.[1] In this he

[1] Bull. Dept. Geol. Univ. Calif., vol. 2, No. 9, pp. 269–314.

gives the following Tertiary section, with which the occurrence of vertebrate and plant fossils is here noted:

Rattlesnake formation: Gravels, ash, tuff, and rhyolitic lava. Vertebrate fauna.
Mascall formation: Ashes, tuffs, and possibly gravels. Vertebrate fauna, and flora.
Columbia lava: Basaltic flows.
John Day series: Ashes, tuffs, and rhyolitic flows. Sands and gravels near the top. Lower, middle, and upper divisions. Vertebrate fauna, and small flora.
Clarno formation: Ashes, tuffs, andesitic and rhyolitic flows. Lower and upper floras.

On the basis of the faunas, and of the floras whose ages were determined by Knowlton, Merriam gave the age of the Clarno formation as Eocene, the John Day series as Oligocene, the Mascall formation as Miocene, and the Rattlesnake formation as Pliocene.

No locality in the West, with the exception of the Florissant beds of Colorado, has furnished so large an amount of well-preserved plant fossils as the John Day Basin. The earlier collections were described by Newberry[1] and Lesquereux,[2] but the first comprehensive study of the floras that took into consideration their stratigraphic sequence was published by Knowlton[3] in 1902. In it he described three floras: the Lower Clarno flora from Cherry Creek, comprising 22 forms, the age of which he placed as Lower Eocene; the upper Clarno flora from Bridge Creek and adjacent localities, comprising 45 forms, which he referred to the Upper Eocene; and the Mascall flora from Van Horn's Ranch, comprising 80 forms, regarded as Upper Miocene.

It will be the purpose of this paper to discuss the middle of these three floras, commonly known as the Bridge Creek flora. This flora is selected because of the large number of individual specimens available for study, and because of the suggestive character of its dominant species. The writer has had access to all of the large collections of this flora in the United States, and has made extensive collections in the course of his work in Oregon during the past four years. In addition to the principal localities of the John Day Basin, at Bridge Creek, Butler Basin, and Clarnos Ferry,[4] several localities on the Crooked River, a few miles east of Post, have furnished an abundance of material. Collections made near Ashland, in the southwestern part of the state, appear also to be closely related to the John Day material.

## PRINCIPLES GOVERNING THE DETERMINATION OF FOSSIL PLANTS.

Before taking up the discussion of the taxonomic characters of the Bridge Creek flora, it may be well to consider certain of the principles that are coming to govern the determination of fossil plant genera

[1] U. S. Nat. Mus. Proc., vol. 5, 1882, pp. 502–14, and U. S. Geol. Surv. Mon. 35, 1898.
[2] U. S. Geol. Surv. Terr. Rept., vol. 8, pp. 239–255, pls. 50–59.
[3] U. S. Geol. Surv. Bull. 204, 1902.
[4] *Ibid*, p. 20.

and species.[1] Earlier workers, of whom Heer and Lesquereux may be mentioned as conspicuous examples, appear to have been handicapped by a lack of knowledge of the distribution of modern plants. As a result it was their practice to recognize in their European or North American floras many genera based on leaf impressions, too often fragmentary, which have a modern range remote from the area furnishing the fossils. In his Tertiary Flora of Switzerland,[2] Heer includes with a large group of temperate genera now common in Europe, such genera as *Diospyros, Myrsine, Grewia, Eugenia, Sterculia, Sapindus, Zizyphus, Paliurus,* and *Cinnamomum.* Lesquereux[3] lists *Ficus, Persea, Aralia,* and *Zizyphus* along with the oaks, willows, poplars, and sycamores which to-day, as in the Tertiary, characterize the region of his Auriferous Gravels flora. Such mixtures of tropical and subtropical genera with temperate genera become increasingly difficult to explain, as also pointed out by Berry,[4] when the Arctic floras are considered, and have led to some climatic speculation which appears hardly to be justified. As a method of procedure, it seems desirable first to take as a list of eligible genera those now occupying the region where the fossils occur; when the possibilities for matching with these have been exhausted, the genera of the surrounding regions may be considered, and next the genera of the continent. There may in some cases still remain fossil forms which have not been placed. Under such circumstances foreign genera may be considered but always with the provision that while trans-oceanic distances in longitude may not present difficulties, like distances in latitudes are ordinarily prohibitive.

This attitude against the inclusion of tropical genera in the Tertiary floras of the West is based on the unmistakably temperate aspect which these floras show. The Bridge Creek flora is characterized by four dominant species, *Sequoia langsdorfii, Alnus carpinoides, Quercus consimilis,* and *Umbellularia* sp.[5] *Sequoia langsdorfii* is closely related to the living redwood, *S. sempervirens; Alnus carpinoides* has many points of resemblance with the living red alder, *A. rubra; Quercus consimilis* is not essentially different from the living tanbark oak, *Q. densiflora;* and *Umbellularia* sp. closely resembles the living California laurel, *Umbellularia californica.* These living species are four of the dominant members of one of the forest associations now living in the West, the coast-range redwood forest which

[1] F. E. Clements, Plant succession, Carnegie Inst. Wash. Pub. No. 242, p. 362, 1916.
F. E. Clements, Scope and significance of Paleo-ecology, Bull. Geol. Soc. Amer., vol. 29, p. 369, 1918.
F. E. Clements and R. W. Chaney, Methods and principles of paleo-ecology, Carnegie Inst. Wash. Year Book No. 22, 1923.

[2] Tertiaer Flora der Schweiz, vols. 1, 2, 3, 1855–59.

[3] Mus. Comp. Zool. Mem., vol. 6, No. 2, 1878.

[4] Proc. Amer. Philos. Soc., vol. 61, 1922.

[5] This and other new species will be described in a later paper.

extends from southwestern Oregon south along the coast of California nearly to the southern end of Monterey County, a distance of 450 miles. The climatic conditions under which this forest now lives are described by Sudworth[1] who states in his description of the redwood that it is "closely confined to humid regions subject to frequent and heavy sea fogs; trees outside this influence are scattered and small. * * * Temperature rarely below 15° or above 100°; annual average from 50° to 60°F. Annual precipitation between 20 and 60 inches, mainly as winter rains."

As would be expected, none of the genera associated with this redwood forest are typically tropical or subtropical in nature; they are all such temperate genera as *Acer* (maple), *Corylus* (hazel), *Pseudotsuga* (Douglas fir), and *Cornus* (dogwood). It seems reasonable to suppose that the genera associated with the Tertiary equivalent of this forest should also have been temperate. It would hardly be expected that *Ficus*, *Cinnamomum*, *Sapindus*, and *Grewia* should have been a part of this forest association during the Tertiary, any more than at present. The use of this ecological method,[2] involving as it does the climatic and distributional requirements of the modern relatives of fossil plants, may then serve to eliminate the unlikely genera, and at the same time to indicate those genera which should be associated with the known dominants.

An example of the application of this method may be cited in connection with the species described as *Cinnamomum bendirei*[3] in the Bridge Creek flora. The Lauraceae, to which family *Cinnamomum* belongs, have their chief centers of distribution to-day in southeastern Asia and Brazil. The 40 genera and 1,000 species are in the main tropical and subtropical. The genus *Cinnamomum* itself is confined to eastern Asia and the East Indies. Consequently the recording of a species of *Cinnamomum* in an assemblage of temperate species in the Tertiary of central Oregon is at once open to suspicion. The general resemblance of *Cinnamomum bendirei* to the leaves of *Cinnamomum camphora*, the modern camphor tree of China and Japan, can not be questioned; but small differences in nervation and general shape may be noted which strengthen the suggestion based on ecologic criteria that the Bridge Creek species is not referable to this genus. The recent finding of a number of small leaves in the deposits at Bridge Creek throws further light on the matter, for while they have the general nervation characters of the typical *Cinnamomum bendirei*, they are wholly unlike any member of the genus in shape. Following the method of procedure above suggested, an effort has been made to establish a relationship between

[1] Forest trees of the Pacific slope, U. S. Dept. Agr., Forest Service, p. 147.
[2] See footnote on p. 5.
[3] U. S. Geol. Surv., Bull. 204, 1902, p. 59, pl. X, fig. 4.

the fossil leaves in question and some genus now living in the western United States. *Philadelphus*, the syringa, is commonly represented in many parts of the West, and occurs within a few miles of the Bridge Creek localty. It is also a characteristic associate of the redwood in California. The fossil leaves appear to resemble those of this redwood associate, *P. lewisii*, much more closely than they do any species of living *Cinnamomum;* the small leaves which are wholly unlike *Cinnamomum* closely resemble the leaves on the fertile shoots of *Philadelphus lewisii;* and the larger fossil leaves are almost identical with the leaves of its sterile shoots. In addition to the leaves there are a number of impressions of buds and seed capsules which suggest those of *Philadelphus.* The evidence based both on the characters of the fossils and the ecologic probabilities seems to justify referring this species to *Philadelphus* rather than to *Cinnamomum.* But it should be pointed out that while the ecologic probabilities have in this case given the initial suggestion of referring these fossil leaves to a temperate rather than to a tropical genus, the fundamental basis for doing so is their morphological resemblance to the leaves of *Philadelphus lewisii.*

It should be mentioned also that leaf impressions which may be referable to the genus *Cinnamomum* have been found in the older Tertiary of Oregon. This presents the possibility that the Bridge Creek flora might include a species of this genus which has remained and established itself under temperate conditions, somewhat after the fashion of *Cinnamomum camphora,* now living in China and Japan, but no such species has yet been found.

The ecological method is of value also in suggesting the reference of leaves described as *Fraxinus integrifolia* to *Umbellularia.* When Newberry described *Fraxinus integrifoila,*[1] he pointed out the fact that there were some reasons for questioning its reference to this genus; and Knowlton[2] shows that the fossil leaves are quite unlike those of *Fraxinus.* Having in mind the probable associates of *Sequoia langsdorfii, Quercus consimilis,* and *Alnus carpinoides,* based on the associates of their modern relatives in the redwood forest, the presence of *Umbellularia* in the Bridge Creek flora seems highly probable. Newberry's figures of *Fraxinus integrifolia* and the hundreds of fossil leaves collected at Bridge Creek closely resemble the leaves of *Umbellularia californica* in shape, nervation, and range of variation, and there can be no reasonable doubt that they should be referred to *Umbellularia* rather than to *Fraxinus.*

A species of alder, *Alnus carpinoides,* has been mentioned as constituting one of the dominants of the Bridge Creek flora. Few botanists would attempt to distinguish certain species of *Alnus* from

[1] Newberry, U. S. Geol. Surv. Mon. 35, 1898, p. 128, pl. XLIX, figs. 1–3.
[2] Knowlton, U. S. Geol. Surv. Bull. 204, 1902, p. 84.

its close relative *Betula* (birch) on the basis of the leaves, which are much alike in these two genera. If the fossil remains consisted only of leaves, it would probably be impossible to determine which of the two genera was represented. But occurring with the leaves are a few aments which are clearly those of *Alnus*, and which indicate without question that this genus was present. And while it is impossible to state that none of the leaves are those of *Betula*, it seems reasonable to assume that most or all of them are *Alnus*. The presence of *Alnus* in the modern redwood forest and the total absence there of *Betula* give further evidence of importance. In the case of *Quercus consimilis*, the generic reference can hardly be questioned, for there is no closely related genus as in the case of *Alnus*. But here, the occurrence of acorns with burr-like cups and elongate nuts confirms the relationship, suggested by the leaves, to the tanbark oak, *Q. densiflora*. Again, the abundant leaves of *Sequoia langsdorfi* can hardly be referred to any other genus. But the presence of cones makes certain the generic reference, and at the same time, because of the small size of the cones, indicates a relationship with the coast redwood, *S. sempervirens*, rather than with the bigtree, *S. gigantea*. The use of fruiting material, unfortunately not as commonly found with fossil leaves as might be wished for corroborating generic references and for suggesting specific relationships, is clearly of great importance in taxonomic work.

Fossil wood, although abundantly represented in many of the Tertiary deposits containing leaf impressions, has been little used as an aid to taxonomic work. This is unfortunate, for the wood characters appear to have diagnostic value in the determination of many genera, and may in some cases be used to distinguish species. The work now in progress is not sufficiently advanced to add any suggestion of relationships based on the stem structures.

A realization of the extent of leaf variation within a species is serving to correct many of the taxonomic errors which have multiplied the species of Tertiary plants. A survey of the plates in the works of Newberry and Lesquereux already cited[1] (especially plates 44, 45, 46, 47, and 49 of Newberry's monograph, and plates 50, 51, and 53 of Lesquereux's Cretaceous and Tertiary Floras) will disclose the considerable number of separately described species, referred to several genera, which show a close similarity. And the types of the specimens there figured, which have been examined by the writer, show an even closer similarity than the figures. Commenting on this situation over 20 years ago,[2] Knowlton writes as follows:

"Lesquereux, through whose hands much of this material has passed, would separate them not only into many species but into several genera (*Quercus*, *Alnus*, *Betula*, *Carpinus*, etc.), while Newberry, judging from what he actually did, would combine them all under

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[1] U. S. Geol. Surv. Mon. 35, 1898, and U. S. Geol. Surv. Terr., vol. VIII, 1883.
[2] U. S. Geol. Surv. Bull. 204, 1902, pp. 39, 40.

his *Populus polymorpha.* I can not believe that they belong to Populus. The only living species with which it is reasonable to compare them is *Populus alba*, which has, it is true, very variable leaves, but they seem of a different type and generically unlike the ones under consideration. I have, therefore, broken up Newberry's *Populus polymorpha*, placing certain of them under this form (*Betula heteromorpha*). If Newberry's elastic species was maintained it would be polymorphous enough to include them all, but I do not think it will adequately represent the facts to do so. In regard to Lesquereux's point of view, it may be said that if extreme examples were selected it might seem logical to call them species, but when the whole are grouped together it is found absolutely impossible to draw any satisfactory line between them. Take, for example, the question of shape. The narrowest possible form may be unlike the broadest form, yet every step between them can be found. So, also, from the specimens with a wedge-shaped base to those with a truncate base, and still farther to those with a markedly inaequilateral base, there are gradual steps. In the matter of nervation, however, there are comparatively slight differences, yet even here the variations are all connected."

If, as Knowlton states, we are dealing with a large number of specimens whose variations intergrade, there can be only two consistent courses, either to call each intergrading type by a separate name, of specific or sub-specific rank, or to assemble them all under one species. The first alternative is impossible, for, with the wealth of material available, there would be scores of such species or subspecies. If the second alternative is sound, the correctness of assembling all of these types under one species can be tested by a study of the variation in a single living species of a likely genus. This genus has already been designated as *Alnus* on the basis of fruiting material which is associated with the leaf impressions; and the resemblance of the fossil form to *Alnus rubra*, the living associate of the redwood, has also been pointed out. Among the living alders, however, *Alnus tenuifolia*, the mountain alder, is much more like *A. carpinoides* than is *A. rubra*, the red alder. These two living species are themselves closely related, *A. rubra* representing a species with a more restricted range than *A. tenuifolia*. Plates 2 to 7 show some of the more common types of variation in the leaves of *A. tenuifolia* collected by the writer from a single living tree in the Blue Mountains less than 15 miles from the Bridge Creek fossil locality, together with corresponding types of variants of *A. carpinoides* from the Bridge Creek flora. With these are shown the original figures of the types of the several species to which these variants have been referred by previous authors. There are also shown variants of another living species, *A. alnobetula,* now found generally distributed in the northern hemisphere, where it is divided into several varieties of which the American form is commonly referred to as *A. sinuata* or *A. sitchensis*. The resemblance between this species and *A. carpinoides* is more marked than in the case of any other living species studied, the margin being closely similar and the range in shape and nervation practically identical. Unfortunately, the only specimens of *A. alnobetula* available for this comparison are herbarium specimens, representing different trees from several

localities in the Northwest. It seems probable that leaves could be selected from a single tree which would show the same range in variation. There are trees of this species now growing on Mount Hood, less than 100 miles distant from the Bridge Creek locality.

The suggestion may be made, on the basis of this variation in the characters of the modern leaves of *Alnus*, that the several fossil species which are included within this range of variation should all be referred to the single species, *Alnus carpinoides*. There should then be eliminated from the Bridge Creek flora the following species: *Betula bendirei, B. heterodonta, B. heteromorpha, B. angustifolia, Alnus macrondonta, Populus polymorpha, Quercus pseudo-alnus,* and probably *Quercus oregoniana*. It is possible that these leaves may belong to more than one species of *Alnus*, but modern forests do not commonly include more than one species of alder, and the presence of more than one species in the Bridge Creek forest seems unlikely in lack of any positive evidence.

Such examples of individual variation in the leaves of living and fossil species of plants do not indicate, as is occasionally maintained by geologists and botanists, that fossil leaves have no critical stratigraphic or taxonomic value. Once the range of variation in a species is established, this species will have greater stratigraphic value than the many species actually representing related variants, which may formerly have been considered to be horizon markers. And as regards the taxonomic aspects of the case, it should again be emphasized that, since in the cases of some plants, both fossil and modern, the leaves do not serve to distinguish species or even genera, it will be necessary in such critical cases to have the additional evidence of the stems and fruits. This additional evidence is fortunately available in all cases with modern plants, and can be made available in the course of time with most of the fossils as well. A sound taxonomic understanding of fossil plants is essential to one of the most important phases of palaeobotany, the interpretation of the plants in relation to the physical conditions which they indicate. It is clearly impossible to make sound deductions as to climate, topography, and conditions of sedimentation from them if a single species of alder is mistakenly considered as several species each of alder, birch, and oak.

From the preceding discussion of taxonomic principles, it is clear that the taxonomic considerations of a fossil flora are inseparable from the ecologic considerations, since the known facts of modern plant association serve as one of the principal bases for determining fossil plants. The Bridge Creek flora has already been described as resembling the modern coast-range redwood forest of the West, on the basis of its most abundant species, *Sequoia langsdorfii, Alnus carpinoides, Quercus consimilis,* and *Umbellularia* sp. The nearly

universal presence of these species in localities tens of miles apart over an area of hundreds of square miles in extent is indisputable evidence that they were well suited to the climatic and topographic conditions which prevailed in central Oregon during this part of the Tertiary.

While in general the abundance of individual specimens of the leaves of a given species may be taken as an index to its dominance in the living flora of its day, there are at least five contributing factors which should be considered in this connection: (1) The distance of the given species from the stream, lake, or other site of deposition of sediments in which the leaves were buried, (2) the original thickness of the leaf, determining its ability to be transported without destruction, (3) the size and shape of the leaf as related to its transportation in the air and the water, (4) the habits of the plant with regard to shedding its leaves, and (5) the height of the stem of the plant, involving its arborescent, shrubby, or herbaceous habit. Clearly a tree with deciduous habit, broad and medium-sized leaves of thick texture, and which grows near the site of deposition will have the best chance of getting its leaves into the sediments to become fossils. Regarding the first factor, it may be assumed that the plants growing on the borders of the site of deposition have the best opportunity to become fossils. Quantitative studies have been begun, by which it is hoped to reach certain conclusions regarding the distance which leaves of various trees may travel before coming to rest. The abundance of *Alnus* in the Bridge Creek collections is surely due in large part to its occurrence around the borders of the water body where the sediments accumulated, and along the streams which flowed into it. But the great number of its leaves in all localities is as certainly an indication of its position in the Bridge Creek flora as a dominant.

This first factor can not explain the abundance of the leaves of *Quercus consimilis*, which is ordinarily not a stream or lake border type. In the modern redwood forest, its relative *Q. densiflora*, grows among the redwoods on the slopes above the streams, or on the upper flats. In the case of this species, the second factor determines in part its numbers in the Bridge Creek collections, for its leaves are of sufficient thickness to withstand a considerable journey, by air or water, without destruction. The assumption of a thick texture is not based on inferences from the texture of the related modern species for the fossil leaves show by their indistinct nervation and their slightly concavo-convex form that they were thick in life. But in any case, *Quercus consimilis* may be considered to have been an abundant tree in order to have distributed its leaves so widely and in such numbers from a habitat probably somewhat removed from the site of deposition. The abundance of *Umbellularia*

appears to be due to the same cause—leaves well adapted to transportation.

*Sequoia langsdorfii* illustrates the application of the third and fourth factors as listed above. A needle-shaped leaf is clearly at a disadvantage for transportation by wind. Especially is this true when the habit of *Sequoia* in shedding its leaves is considered, for in falling they commonly remain attached to the small terminal branches whose weight seldom permits them to fall far from the parent tree. Although *Sequoia langsdorfii* may be supposed to have been the most abundant tree in the Bridge Creek forest, as is the redwood in the Redwood Belt to-day, there are over three times as many leaves of the alder in the shales at Bridge Creek. This indicates not that the alder was more abundant but that its leaves were better suited for transportation. Presumably the leaves of *Sequoia langsdorfii* entered the sedimentary record largely from trees whose branches extended out over the streams and lakes.

There is another aspect of the fourth factor, regarding the habits of the plant with relation to the shedding of its leaves. In the case of herbs, the leaves are commonly not shed, but dry up or are killed by the frost. As a result they are seldom preserved as fossils. In this connection, the fifth factor, having to do with the height of the stem of the plant, is also applicable, for the short stems of herbs do not favor long journeys by wind on the part of such leaves as may become loosened. As a result, ferns and other herbs are much less common in fossil deposits than their actual abundance in the plant associations of the past would seem to call for.

## COMPOSITION OF THE BRIDGE CREEK FLORA.

From the consideration of these factors it appears certain that *Alnus carpinoides*, *Quercus consimilis*, *Umbellularia* sp., and *Sequoia langsdorfii* all were abundant and characteristic species of the forest during the Bridge Creek epoch, as may also have been certain other species less favored for entering the sediments and leaving their impressions. What genera these species were likely to have represented may be suggested by the present-day associates of these dominants in and on the border of the redwood forest of California. Recent studies by the writer in this forest from San Francisco Bay to the northern part of the state, together with suggestions by Dr. W. L. Jepson, have furnished the following list of species. Accompanying this list is the list of equivalent species which occur in the Bridge Creek flora, with the percentage of each as observed in the course of a recent count of over 20,000 specimens at the type locality on Bridge Creek. Several of the species listed below were not found during the count at the type locality, and in the case of these the locality and the approximate number of individuals seen is recorded in the footnotes.

| *Modern Redwood Forest.*[1] | *Bridge Creek Flora.* | p. ct. |
|---|---|---|
| Picea sitchensis Carr. (Sitka spruce). | | |
| Tsuga heterophylla Sarg. (Hemlock) | Tsuga sp.[3] | |
| Pseudotsuga taxifolia Britt. (Douglas fir). | | |
| Abies grandis Lindl. (Grand fir). | | |
| Sequoia sempervirens Endl. (Redwood) | Sequoia langsdorfii Heer | 15 |
| Torreya californica Torr. (California nutmeg) | Torreya sp.[4] | |
| Myrica californica Cham. (California myrtle) | Myrica sp. | .03 |
| Corylus rostrata Ait. var. californica (California hazel) | Corylus macquarrii Heer | .01 |
| Alnus rubra Bong. (Red alder) | Alnus carpinoides Lesq. | 53.87 |
| Castanopsis chrysophylla A. DC. var. minor (Chinquapin). | | |
| Quercus[2] densiflora Hook and Arn. (Tanbark oak) | Quercus consimilis Newb. | 8.92 |
| Berberis nervosa Pursh. (Oregon grape) | Berberis simplex Newb. | .01 |
| Umbellularia californica Nutt. (California laurel) | Umbellularia sp. | 8.82 |
| Acer macrophyllum Pursh. (Broad-leaf maple) | Acer osmonti Kn. | .67 |
| Acer circinatum Pursh. (Vine maple). | | |
| Rhamnus purshiana DC. (Cascara Sagrada) | Rhamus sp.[5] | |
| Cornus nuttallii Aud. (Western dogwood) | Cornus sp. | .04 |
| Rhododendron occidentale Gray. (Western Azalea). | | |

Of the total of 18 species listed for the modern redwood forest, 12 are represented by equivalents in the Bridge Creek flora. Of these, the 4 which are most abundant, *Alnus carpinoides*, *Sequoia langsdorfii*, *Quercus consimilis*, and *Umbellularia* sp. represent the 4 species which are among the most common in the modern forest, and which appear for reasons discussed to have been most favorably situated to leave a record in the Bridge Creek sediments. Only 3 of the 6 coniferous species of the modern forest are recorded in the Bridge Creek flora, and one of these, *Tsuga heterophylla*, has its fossil equivalent represented by only a single specimen. The rarity or absence of all of the conifers excepting *Sequoia* in the Bridge Creek flora is probably due largely to the habits of these genera in shedding their leaves. Unlike the *Sequoia*, which sheds the whole twig and thus makes a conspicuous fossil, the others shed their leaves a needle at a time. Single needles are rather commonly met with in the leaf shales, but they do not possess characters which make them determinable. The specimens of *Torreya* and the single specimen of *Tsuga*, from which over half of the needles have been shed, probably represent the accidental breaking off of twigs which subsequently entered the deposits. As previously pointed out, the twigs of conifers are not as well fitted to be transported widely by air or water currents as are the broader leaves of the angiosperms. The scarcity of coniferous fossils in the flora is therefore readily explained; *Sequoia* itself would have been less common were it not for its habit of shedding needle-bearing twigs, and for its dominance in the Tertiary forest.

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[1] This forest is only one of the units of the coniferous forest of the western United States, and may be accurately termed the *Sequoia* consociation of the coast forest climax.

[2] The generic name *Lithocarpus* is sometimes used, to emphasize the intermediate position of this form between the oaks and the chestnuts. But the name *Quercus* is retained here to correspond with the generic reference of the fossil equivalent.

[3] 1 specimen, Crooked River.

[4] 2 specimens, Crooked River.

[5] 5 specimens, Ashland.

The scarcity of *Myrica* may be in part explained by the fact that it is a shrub, and that it does not grow commonly on the stream borders. *Corylus* also may owe its rarity to its shrub habit, but its present abundance near streams in the redwood forest would lead one to expect a larger fossil representation. The probable absence of *Castanopsis* may be due to its being a shrub, and to the fact that its occurrence was for the most part away from stream borders. There are, however, a number of fossil leaves which may ultimately be referred to this genus. *Berberis* was at a still greater disadvantage with regard to entering the record, for it is an undershrub. Leaves of *Acer osmonti* are surprisingly rare, although *Acer* seeds which are probably referable to this species are fairly common. In the modern forest, *Acer macrophyllum* grows best on the slopes above the streams, which may in part account for the scarcity of its Bridge Creek equivalent in the fossil record. *Acer circinatum* is present to-day only in the northern portion of the redwood forest, and may perhaps be a relatively recent boreal addition. It is of interest to note that it is represented in the Mascall flora of the John Day Basin, which is of Miocene age. The rarity of *Rhamnus* and *Cornus* in the Bridge Creek record is probably due in large part to the fact that they were shrubs. The absence of a representative of the genus *Rhododendron* in the Bridge Creek flora is surprising in view of the abundance of *Rhododendron occidentale* along the stream borders in the redwood forest of to-day. Since there is no fossil record of the genus in North America, it may be supposed that it is a comparatively recent arrival from eastern Asia, which is its present center of abundance.

In addition to this group comprising the redwood and its typical associates, there are a number of other species which are found to-day not far from the redwood forest on the more open slopes or in the open stretches of the valleys. The list of these follows, together with the Bridge Creek equivalents and the percentage data.

| *Modern Redwood Forest Border.* | *Bridge Creek Flora.* | p. ct. |
|---|---|---|
| Pinus ponderosa Laws. (Western yellow pine) | Pinus knowltoni Chaney.[2] | |
| Salix sitchensis San. (Silky willow). | | |
| Populus trichocarpa Hook. (Black cottonwood). | | |
| Quercus garryana Hook. (White oak). | | |
| Quercus chrysolepis Leibm. (Canyon live oak). | | |
| Quercus kelloggii Newb. (Black oak). | | |
| Philadelphus lewisii Pursh. (Syringa) | Philadelphus sp | 0.28 |
| Pyrus rivularis Roem. (Oregon crab apple). | | |
| Crataegus rivularis Nutt. (Hawthorn) | Crataegus newberryi Cock | .35 |
| Holodiscus discolor Maxim. (California meadow sweet). | | |
| Rosa nutkana Presl. (Wild rose) | Rosa hilliae Lesq | .05 |
| Aesculus californica Nutt. (California buckeye). | | |
| Fraxinus oregona Nutt. (Black ash) | Fraxinus sp | .12 |
| Arbutus menziesii Pursh. (Madroño)[1]. | | |

[1] There are a few fossil fragments which may be referable to this genus.
[2] 1 specimen, Crooked River.

As might be expected, there are fewer equivalents of this border group in the Bridge Creek flora, and in no case is one of these represented by many individuals. In addition to the fact that all of these may be supposed to have lived in a situation apart from the Bridge Creek basin of deposition, over half of them are shrubs whose leaves would not ordinarily travel widely. But although this group is of no great importance in the Bridge Creek flora, it is of interest to note that it is well represented in the Mascall flora, a younger flora of the John Day Basin, and in the Eagle Creek flora, one of equivalent or younger age in the Columbia River Gorge, a little over 100 miles to the northeast. In them, *Pinus*, *Salix*, *Populus*, 2 species of *Quercus*, *Crataegus*, and *Aesculus* are represented, in addition to at least 5 of the species of the typical redwood group. *Quercus pseudolyrata*, the equivalent of *Q. kelloggii*, is the most abundant species. Clearly these latter two floras represent a more open type of forest than that which lived during the earlier Bridge Creek epoch.

Mention should here be made of several herbaceous forms. For reasons previously discussed, herbs are rare in fossil floras, and the occasional record of their presence is of all the more interest. There are half a dozen or more specimens which can be referred to *Pteris*, according to Mrs. Carlotta C. Hall. This fern is common in the more open places in the redwood forest as well as elsewere. A single stem of *Equisetum* has been recognized, a plant which may be supposed to have grown during the Bridge Creek epoch, as to-day, on the forest borders and stream banks. One of the most common herbs in the redwood forest is *Asarum caudatum*, the wild ginger. From the characteristic nervation of a single fossil leaf, it appears likely that this genus had a representative in the Bridge Creek flora, but until more fossil material is available this reference must remain slightly uncertain.

Altogether the Bridge Creek flora contains a representative group of the species now found in the redwood forest of California and on its borders. It seems likely that the absence of certain species now associated in the redwood forest is due in part to their failure to enter the fossil record, as in the case of the conifers other than *Sequoia*, and in part to their actual absence from central Oregon during this part of the Tertiary. If it is supposed that certain members of the modern forest were lacking, it seems reasonable to assume that other species not now associated with the redwood may have been present. There are at least four such species in the Bridge Creek flora which have no generic representatives in the modern redwood forest, though all the genera to which they belong are represented in other living forest communities of the West. Of these there are 2 species of *Platanus* (sycamore), one of which is related

to the living western species, *P. racemosa,* and the other of which more closely resembles species now found in Asia and in eastern North America. There is a species of *Juglans* (walnut) which is not unlike several American species now living. And there is a species of *Celtis* (hackberry) which resembles the western species of this genus much more closely than those now living in the eastern United States. Of this group of species, the sycamores are most abundant, *Platanus condoni* comprising 0.90 per cent and *Platanus aspera* 1.14 per cent of the total in the count made at the type locality. The other two are poorly represented, *Juglans* comprising 0.26 per cent and *Celtis* 0.03 per cent of the total.

In addition to the group of Bridge Creek species above named, whose modern representatives are members of the living redwood forest, or are at least found in the West to-day, there is another group made up of four species which do not have generic representatives in the western part of North America at the present time. A list of these follows, with their percentages in the count at Bridge Creek and with their most nearly related living species:

| *Bridge Creek Forms.* | | *Related Living Species.* |
|---|---|---|
| Carpinus grandis................ | 0.05 per cent | Carpinus caroliniana Walt. |
| Fagus[1] sp...................... | | Fagus grandiflora Ehrh. |
| Ulmus speciosa.................. | 2.17 per cent | Ulmus americana L. |
| Tilia sp........................ | .35 per cent | Tilia glabra Vent. |

The related living species are all a part of the moist forest of the northeastern United States.[2] whose climatic and topographic requirements are not essentially different from those of the redwood forest. The inclusion of these Tertiary equivalents in the Bridge Creek flora offers an interesting problem in view of their present absence from the Pacific Coast.

The Tertiary floras of Eurasia and Greenland also have a bearing on this problem. The floras described by Heer from Switzerland and the Arctics,[3] and the flora recently described by Florin from southern Manchuria,[4] include many of the typical Bridge Creek species whose modern relatives make up the redwood forest. In addition they contain some of these species of which the modern relatives are now limited in North America to the eastern part; closely related living species are found also in western Europe and in eastern Asia under climatic conditions similar to those in the eastern United States. It seems reasonable to suppose that during at least the middle part of the Tertiary a habitat similar to that of the Coast Ranges in California prevailed over much of the northern

[1] Not found at Bridge Creek. Six specimens at the Crooked River locality.

[2] *Fagus grandiflora* goes as far west as the Mississippi River, while the other three species extend west of the Missouri.

[3] Tertiaer Flora der Schweiz, 1855–59, and Flora Fossilis Arctica, 1868–83.

[4] Geol. Surv. China, Series A, vol. I, Fasc. 1: Zur Alttertiaren Flora der südlichen Mandschurei, 1922.

hemisphere. It may be suggested that the factors which caused the restriction of this wide-spread forest to the present coastal strip of California may also have resulted in the removal from the Pacific Coast of the group comprising *Carpinus*, *Fagus*, *Ulmus*, and *Tilia*.

There is a notable relationship between the Bridge Creek flora and the living flora of eastern Asia. With the exception of *Sequoia*, there are living members of each of the Bridge Creek genera now living there. Two of the four living species of *Torreya* are confined to Asia. *Alnus alnobetula*, which lives in Asia, North America, and Europe, is to be distinguished with difficulty from the Bridge Creek alder. One of the common Asiatic hazels is a variety of the same species that lives in North America, *Corylus rostrata*, to which the fossil species is related. Oaks of the *densiflora* type, comprising the genus *Lithocarpus*, are confined to Asia, with the exception of the one American species which grows mainly with the redwood and has as its Tertiary equivalent *Quercus consimilis*. *Mahonia*, the sub-genus of *Berberis* to which the living and fossil leaves of the Oregon grape belong, is most widely developed in Asia. The fossil hawthorn appears to be more closely related to the Asiatic species, *Crataegus pinnatifida*, than to any other living species. *Platanus aspera*, the most abundant fossil sycamore, is much more like the Asiatic species, *P. orientalis*, than like the modern sycamore of the Pacific Coast.

It is desirable also to point out that the following Bridge Creek genera still live in central Oregon: *Pinus*, *Tsuga*, *Alnus*, *Corylus*, *Quercus* (several species unlike the fossil species), *Celtis*, *Acer*, *Philadelphus*, *Rosa*, and *Cornus*. These are in the main confined to mountains where the moisture conditions come nearest to those of the Bridge Creek epoch, and it is probable that they have existed there continuously since the Tertiary, undergoing specific modifications in most or all cases, as a result of climatic changes.

## CLIMATIC AND TOPOGRAPHIC INDICATIONS OF THE FLORA.

From the foregoing analysis of the more important elements of the Bridge Creek flora, it seems clear that its topographic and climatic setting must have been essentially like that of the modern coast range redwood forest which it so closely resembles. This conclusion is based not only on the presence of a fossil redwood in the Bridge Creek flora, but also on the association with it of a large percentage of the forms now making up the redwood forest, which have similar topographic and climatic requirements. In his discussion of the redwood[1] Professor Jepson has written as follows:

> "The Redwood is an inhabitant of the humid coast region of California from the southwestern corner of Oregon to Monterey County and thus is confined mostly to a narrow strip 450 miles in length and averaging 20 miles in width, which is called the Redwood Belt. In the belt proper the trees grow on the slopes of canyons and river flats of streams belong-

[1] Willis Linn Jepson, The Silva of California, Mem. Univ. Calif., vol. 2, pp. 128, 129, 132

ing to the outer or seaward Coast Range facing the ocean. * * * The altitudinal range is from sea-level to about 3,000 feet. * * * The Redwood Belt is as distinctly marked by its physical and climatic characteristics as it is by the presence of Redwood trees. It is distinguished as a region of high rainfall in the rainy season, of prevailing fogs in the dry season, and of slight changes of temperature during each day and during each year. * * * The main portion of the 'Redwood Belt' from Sonoma County to Del Norte County receives on the coast line a seasonal average of 50 inches of rain. This average is doubtless higher in the extreme north and also inland towards the summits of the mountains. Southward the average decreases rapidly, being 27 inches at Santa Cruz and 15 inches at Monterey. The number of foggy days in the summer months is twice greater than in the winter months, and the actual number of foggy days in the dry season is probably greater in the south than in the north. Summer fogs not only provide a humid atmosphere but the fog particles are mechanically collected by the towering columns of foliage and precipitated in the form of gentle rain. * * * The greatest rainfall in this region is from December to March."

The question may be raised whether the Tertiary redwood forest lived under these identical conditions. It seems possible that the modern redwood forest would thrive in a region without ocean fogs if the aggregate annual rainfall was sufficient and if its distribution throughout the year was essentially uniform. *Sequoia sempervirens* grows successfully in the southeastern United States and in the temperate countries of Europe, under cultivation. The suggestion may, therefore, be made that the Bridge Creek forest and its Eurasian and Arctic equivalents may not have developed exclusively on ocean borders, but may also have lived inland under suitable moisture conditions. Too little is known at the present time about the palaeogeography of central Oregon during the Tertiary to present direct evidence as to the relation of sea and land there during the time the Bridge Creek flora lived. In any case, whether coastal or inland, the Bridge Creek forest seems to have existed in a moist climate with mild and equable temperature and, from the topographic distribution of the living forest which it so closely resembles, it may be supposed to have occupied river valleys and their tributaries up to an altitude of about 3,000 feet.

These suggestions as to the probable climatic conditions under which the Bridge Creek flora lived are wholly out of accord with those made by Calkins.[1] In his discussion of the conditions of accumulation of the Tertiary deposits of the "red beds" of the Lower John Day series, he states his belief that "the early John Day was a period when thin showers of ash were falling with intervals generally long enough to allow oxidation pari passu with their accumulation. The climate was presumably hot and arid, for the iron seems to be in a condition of low hydration." This disagreement tends merely to emphasize the fact that "red beds" do not necessarily indicate an arid climate.

[1] Contribution to the petrography of the John Day Basin, Univ. Calif. Publ. Bull. Dept. Geol., vol. 3, No. 5, pp. 171–172.

## MODE OF DEPOSITION OF THE BRIDGE CREEK SHALES.

In considering the origin of the shales containing the Bridge Creek flora, there must be kept in mind not only the physical indication of the flora, but also the lithologic characters of the deposits containing it, and their geographic distribution. An analysis of specimens of shale from several localities, made for the writer at the sedimentation laboratories of the State University of Iowa, indicates that it is composed largely of ash and pumice, with a siliceous cement. Evidences of lamination are commonly not present, and are in no case conspicuous. Approximately 95 per cent of the ash is below 0.02 mm. in diameter; certain of the larger grains, with a diameter between 0.05 and 0.23 mm. have fine stringy appendages.

The leaf shales occur in layers from a few inches to several feet in thickness, but usually they are not more than a foot thick. The layers of leaf-bearing shales are separated by beds of fine yellow clay up to a foot in thickness at the locality on Bridge Creek, and with these clay beds have a total thickness of at least 40 feet. At Clarnos Ferry and at Grays Ranch on the Crooked River, the intervening clays are more coarse and have a greater thickness than at Bridge Creek; they appear to contain some volcanic material, but to be largely the products of weathering. Horizontally, the leaf shales do not appear to extend for great distances, comprising areas which occur commonly as hills because of their superior hardness. These areas are probably not continuous for more than a few hundred feet, and are surrounded by the banded reddish and yellowish shales which are characteristic of the Lower John Day series.

There are several reasons for supposing that the leaf shales represent sub-aqueous deposits. No considerable amount of the shales has been examined at any locality without finding fragmentary remains of fish. The position of the leaves, which is invariably flat and parallel with the bedding, is not consistent with a sub-aerial site of deposition in which the leaves would be curled from drying and scattered irregularly through the shale. The patchy distribution of the leaf shales suggests deposition in depressions, where fine material accumulated in relatively still water. The lack of agitation during deposition is also indicated by the presence, already noted, of stringy appendages on some of the larger ash particles. The presence of laminae in certain of the shales, and of well-developed bedding planes in all of them is indicative of water deposition.

Deposits of this general type are commonly considered to be of lacustrine origin. This origin can not be applied to the John Day deposits in general, but they contain vertebrate remains which show evidence of at least temporary exposure on a land surface.[1] Rather

[1] See Merriam, Contribution of the geology John Day Basin, Univ. Calif. Publ. Bull. Dept. Geol., vol. 2, No. 9, pp. 299–302.

it seems preferable to consider that they all, including the leaf shales, were deposited in broad valleys. In a sense the leaf shales were doubtless lacustrine, in that they accumulated in the depressions along the courses and borders of the streams. But if these depressions are to be considered as lakes, they must be supposed to have been of a temporary nature, conditioned by the shifting of the stream courses. It seems rather better to call the areas in which the leaf shales accumulated basins of deposition. In their quiet waters the fine volcanic products settled and embedded the leaves and other parts of the plants which were blown or washed in from the adjacent land surfaces. These plants, as has been stated, are distinctly of the valley type in terms of their modern ancestors.

The uniformly fine character of the shale, and the total lack of other than volcanic products in it, may be due to either of two causes. Either the ash and pumice were dropped directly upon the water surface of the basin, each layer representing a single accumulation at its bottom, or they were washed into the basin from surrounding land surfaces which were covered by pyroclastic deposits. The first alternative seems somewhat unlikely as the sole mode of accumulation, in view of the abundance of leaves scattered through the ash, unless each eruption took place in the autumn when there was an abundant supply of loose leaves. It is possible, to be sure, that the leaves were stripped from the trees in the course of the ash fall, but many of them have complete petioles and they do not commonly show signs of abrasion. Unquestionably, in the course of an eruption, a certain amount of ash would have fallen on the surface of the water bodies and have settled to their bottoms. But it seems probable that most of it was washed in from the adjacent ash-covered land surfaces, for a period of months or a few years following the eruption. During this time, leaves shed in a normal fashion during one or more autumns were blown to the basins of deposition, or washed into it by the streams. There is more than a suggestion of such fluctuation in the supply of leaves in the concentration of leaf impressions at certain levels in a layer of leaf shale, and their relative scarcity immediately above and below.[1] As soon as the higher points about the Bridge Creek basins of depositions were denuded of ash, the ordinary products of rock decay became a part of the deposits and the ash became relatively inconspicuous. According to this interpretation, each of the layers of leaf shales represents the time during and immediately following an eruption of ash, and each

[1] About fifteen months after the eruption at Katmai, the writer noted that with a few exceptions the surface of a portion of the island of Kodiak, about 80 miles distant, was still covered with ash, and that in practically none of the gullies had the streams cut through it. It seems certain that the stream deposits here for a period of over a year were as exclusively made up of volcanic products as the leaf shales containing the Bridge Creek flora. It is hoped that subsequent studies in the Katmai region will show to what extent modern leaves have been preserved in these recent deposits.

layer of dominantly non-volcanic shale overlying represents the time between eruptions when the streams were transporting the usual products of rock decay. During these latter times, few or no leaves were preserved in the deposits because of the coarseness of the sediments.

While it can not be positively determined whether the Bridge Creek forest occupied only the upper canyons, or whether it extended down to the borders of the basins of deposition in the larger valleys, several suggestions may be made which indicate that the latter was the case. The abundance of remains of redwood indicates that there were redwood trees growing near the basins of deposition. In the modern forest, this species has its best development along the flats of the larger streams; and it has already been pointed out that the twigs bearing the needles of the redwood are not particularly well fitted for long transportation. The modern representative of two other abundant Bridge Creek species, the alder (*Alnus carpinoides*) and the laurel (*Umbellularia* sp.) are found most commonly in the living redwood forest on the borders of the main streams. Another indication that the broader valleys were covered with forests may be seen in the scarcity of mammalian remains in the Lower John Day series. If these valleys had been occupied by grasslands the mammalian record would unquestionably be more extensive.

## CORRELATION.

No attempt will be made in this paper to reach a final decision as to the age of the Bridge Creek flora. With the completion of a piece of cooperative work at present being carried on under the direction of Dr. Merriam, by Dr. Stock and Dr. Buwalda of the University of California, by Dr. Wright of the Geophysical Laboratory, and by the writer, it is hoped that the detailed stratigraphy of the John Day Basin will be worked out in connection with the mapping and with the studies of the faunas and floras. The suggestion may be made at this time, however, that the flora is probably younger than has been formerly supposed. On lithologic and stratigraphic grounds, it does not seem possible to draw a line between the leaf shales and the lower John Day beds with which they are associated. At the Grays Ranch locality on the Crooked River, which occupies the next basin south of the John Day River, the leaf layers lie several hundred feet above the base of shales which, from their lithology and topographic expression as well as their stratigraphy, appear to be typical Lower John Day. At the type locality on Bridge Creek, and near Clarnos Ferry, leaf shales are associated with what appear to be Lower John Day beds in such a way as to make no line of division possible. The presence in the Bridge Creek flora of certain Upper Eocene species has been noted,[1] but in view of later work the Bridge Creek flora appears to

[1] Knowlton, U. S. G. S. Bull. 204, p. 104, 105.

be more closely related to the Miocene floras of the West than to Eocene floras. From the modern aspect of many of the Bridge Creek species, there seems to be no reason why the flora should not be referred to the Lower John Day beds, commonly considered to be Upper Oligocene in age rather than to the Clarno formation which has been called Eocene.

## SUMMARY.

The Bridge Creek flora is found in Oregon in beds of probable Oligocene age, and a similar group of plant fossils is scattered widely in the Tertiary of the northern hemisphere. It has as its most conspicuous element a group of species whose modern relatives are the important members of the redwood forest, now limited to the Coast Ranges of California. Other species occur which are not found in this forest or even in the Western United States at the present time, but none of these is numerically important. Because of this relation to the redwood forest, the physical conditions under which the Bridge Creek forest lived may be suggested. The climate appears to have been temperate and moist. The shales containing the Bridge Creek fossils are made up largely of volcanic material which was blown and washed into basins of deposition in forested valleys.

FIG. 1. Type locality of Bridge Creek flora in John Day Basin, Oregon. The vegetation is *Artemisia tridentata* (sagebrush) and *Agropyrum spicatum* (wheat grass), with an occasional tree of *Juniperus occidentalis* (western juniper).

FIG. 2. Redwood forest at Muir Woods, California, showing *Sequoia sempervirens* associated with *Alnus rubra* (red alder), *Quercus densiflora* (tanbark oak), and *Umbellularia californica* (California laurel).

1

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2

4

Fig. 1. *Alnus carpinoides* Lesq. Fossil specimen collected by writer at Bridge Creek locality, showing ovate type of leaf, with an asymmetrical cuneate base.

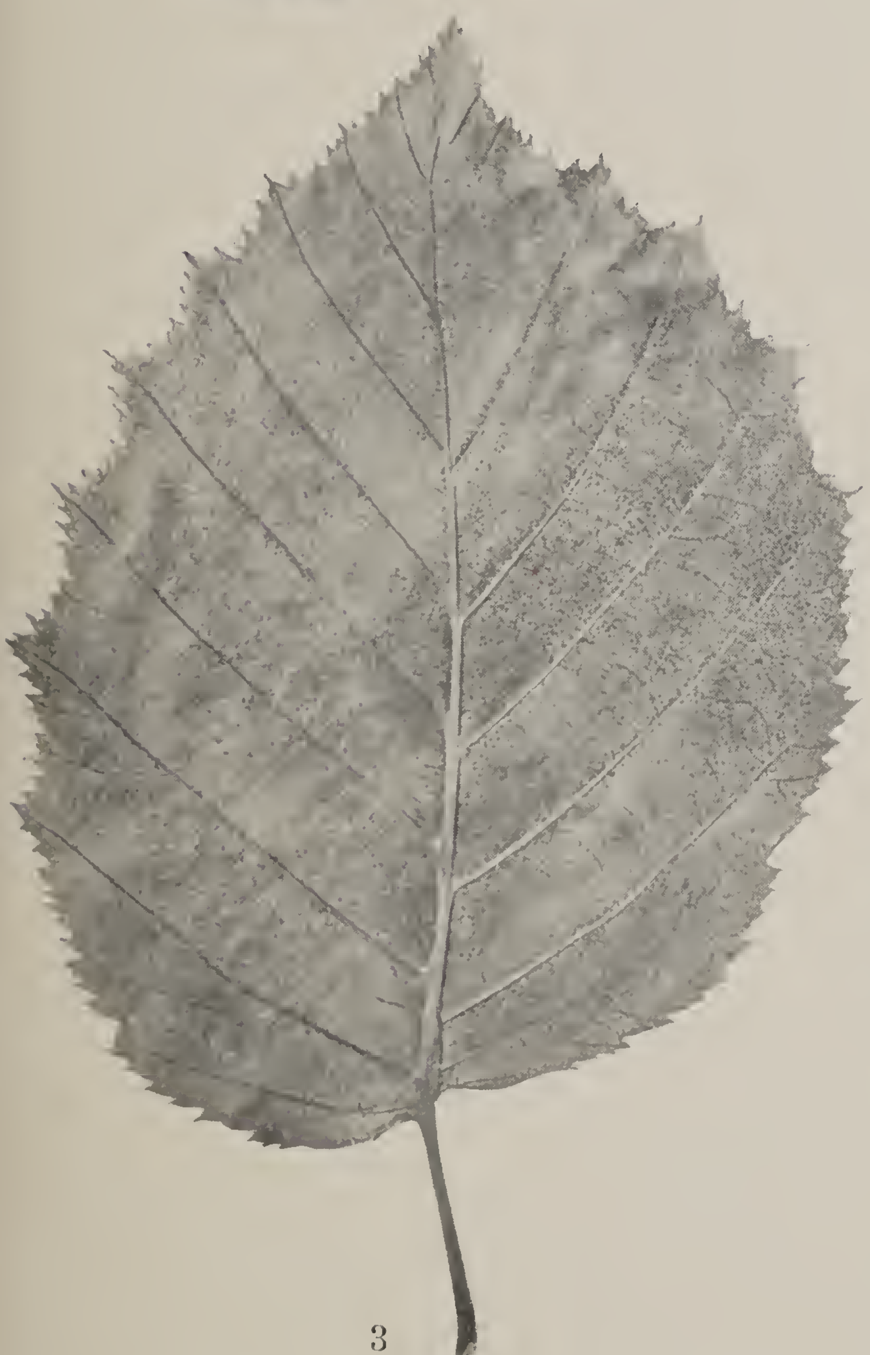
Fig. 2. *Alnus carpinoides* Lesq. Copy (reversed) of one of Lesquereux's type figures, in his Cretaceous and Tertiary Floras, pl. 50, fig. 11.

Fig. 3. *Alnus alnobetula* Ehrh. Specimen of living species in herbarium of Stanford University; collected in Siskiyou Mountains, Oregon.

Fig. 4. *Alnus tenuifolia* Nutt. Specimen of living species collected by writer from a tree in the Blue Mountains about 15 miles from Bridge Creek locality. The examples of *A. tenuifolia* on the following plates are from same tree.

1

2



3

4

Fig. 1. *Alnus carpinoides* Lesq. Fossil specimen collected by writer at Bridge Creek locality, showing more roundly ovate type with an asymmetrical cordate base. Details of margin of this and other fossil specimens are not perfectly preserved.

Fig. 2. *Alnus macrodonta* Kn. Copy of Knowlton's type figure in Bull. 204, U. S. Geol. Surv., pl. 4, fig. 1.

Fig. 3. *Alnus alnobetula* Ehrh. Specimen of living species in herbarium of California Academy of Sciences; collected near Embro, Washington.

Fig. 4. *Alnus tenuifolia* Nutt. Specimen of living species collected by writer from tree in Blue Mountains about 15 miles from Bridge Creek locality.

1

2

3

4

Fig. 1. *Alnus carpinoides* Lesq. Fossil specimen collected by writer at Crooked River locality, showing circular type of leaf with a symmetrical subtruncate base.

Fig. 2. *Betula bendirei* Kn. Copy (reversed) of Knowlton's type figure in Bull. 204, U. S. Geol. Surv., plate 4, fig. 2.

Fig. 3. *Alnus alnobetula* Ehrh. Specimen of living species in herbarium of Stanford University; collected on Mount Hood, Oregon.

Fig. 4. *Alnus tenuifolia* Nutt. Specimen of living species collected by writer from living tree in the Blue Mountains, about 15 miles from Bridge Creek locality, and about 25 miles from Crooked River locality.

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FIG. 1. *Alnus carpinoides* Lesq. Fossil specimen collected by writer at Crooked River locality showing ovate type of leaf with a symmetrical cordate base.

FIG. 2. *Betula heterodonta* Newb. Copy of one of Newberry's type figures in Mon. 35, U. S. Geol. Surv., pl. 44, fig. 3.

FIG. 3. *Alnus alnobetula* Ehrh. Specimen of living species collected near Kootenay, B. C.

FIG. 4. *Alnus tenuifolia* Nutt. Specimen of living species from Blue Mountains about 15 miles from Bridge Creek locality, about 25 miles from Crooked River locality.

1

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Fig. 1. *Alnus carpinoides* Lesq. Fossil specimen collected by writer at Crooked River locality, showing ovate type of leaf with a slightly asymmetrical subtruncate base.

Fig. 2. *Betula heteromorpha* Kn. Copy of one of Knowlton's type figures in Bull 204, U. S. Geol. Surv., pl. 3, fig. 6.

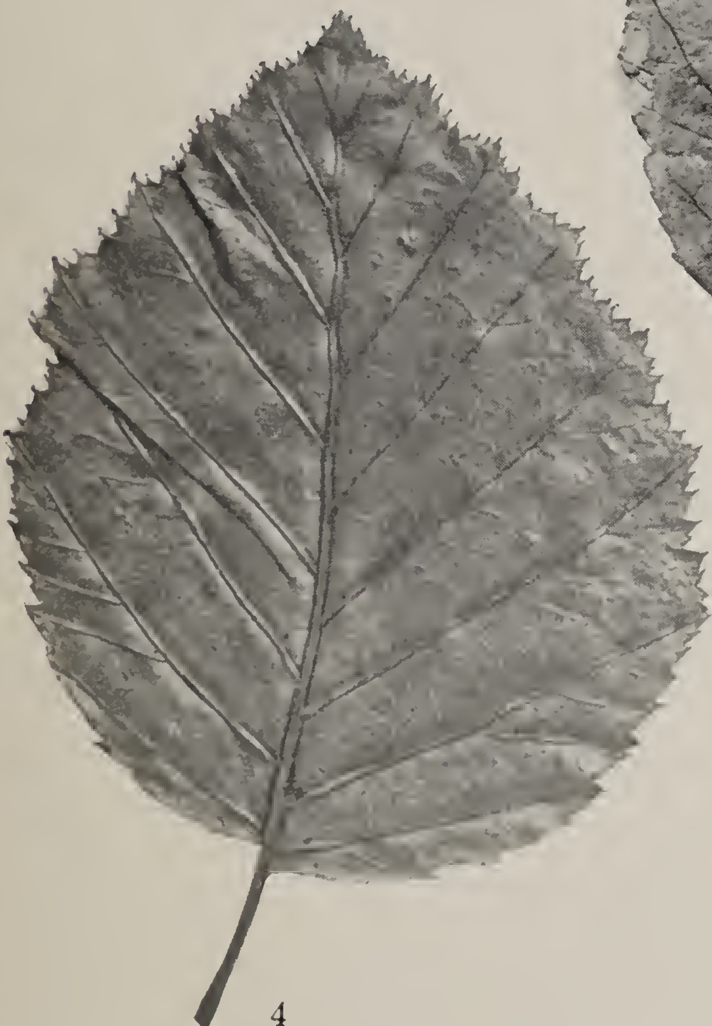
Fig. 3. *Alnus alnobetula* Ehrh. Specimen of living species in herbarium of Stanford University; collected near Midvale, Montana.

Fig. 4. *Alnus tenuifolia* Nutt. Specimen of living species collected by writer from the tree in the Blue Mountains about 15 miles from Bridge Creek locality, and about 25 miles from Crooked River locality.

2

3

1



4

5

FIG. 1. *Alnus carpinoides* Lesq. Fossil specimen from Bridge Creek locality, showing round type of leaf with a symmetrical subtruncate base.

FIG. 2. *Quercus pseudo-alnus* Ett. Copy of a figure used by Lesquereux in his Cretaceous and Tertiary Floras, pl. 53, fig. 6.

FIG. 3. *Populus polymorpha* Newb. Copy of one of Newberry's type figures in Mon. 35, U. S. Geol. Surv., pl. 49, fig. 7. In his Flora of the John Day Basin, Knowlton pointed out that this specimen was identical with those figured as *Quercus pseudo-alnus* by Lesquereux.

FIG. 4. *Alnus alnobetula* Ehrh. Specimen of living species in herbarium of California Academy of Sciences; collected in Kitsap County, Washington.

FIG 5. *Alnus tenuifolia* Nutt. Specimen of living species collected by writer from tree in Blue Mountains about 15 miles from Bridge Creek locality.

II.

# THE MASCALL FLORA—ITS DISTRIBUTION AND CLIMATIC RELATION.

By RALPH W. CHANEY.

With one plate and one figure.

# II. THE MASCALL FLORA—ITS DISTRIBUTION AND CLIMATIC RELATION.

By Ralph W. Chaney.

The Mascall flora is one of the most widespread Tertiary floras of the western United States. During the more than 20 years since it was described by Knowlton[1] from the John Day Basin, this flora has been found in several other localities in Oregon, as well as in Washington, Idaho, Nevada, and California. The purpose of this paper is to record its geographic distribution as now known, and to discuss its age relations and physical indications.

The type locality of the Mascall flora is located on the Van Horn ranch, now owned by Jerome Moore, 12.5 miles east of Dayville, Oregon, on the East Fork of the John Day River. Here a cliff has been cut on the north bank of the river, exposing a section of more than 100 feet of leaf-bearing diatomaceous shale. This locality furnished material for many of the earlier collections, including part of those made by Knowlton and Merriam in 1900. A short distance to the east there are several other localities from which leaf impressions have been collected. The most important of these is on the western-most of two white hills, a mile east of the type locality and on the north side of the river. Knowlton and Merriam secured most of their material here, and collections have also been made by the writer in recent years. The exposed portion of the Mascall formation is about 200 feet thick at this point, and is overlaid a short distance to the east by the Rattlesnake formation. Its lower contact is not visible here, but 6 miles to the west diatomaceous shale containing typical Mascall species lies upon the Columbia lavas. The leaves at the White Hills locality occur in thinly bedded diatomaceous ashy shales, interlayered with fine gray sands, at an elevation of about 125 feet above the river. They comprise the same assemblage of species which has been recorded from the nearby locality at Van Horn's ranch, and for this reason the collections from these two localities will here be considered together, as they were by Knowlton in his Fossil Floras of the John Day Basin.

The writer has recently had an opportunity to look over the Mascall collections at the National Museum, and at various times in the past few years has studied Mascall material in the collections of

[1] F. H. Knowlton, U. S. Geol. Surv. Bull. 204, 1902.

the New York Botanical Garden, the American Museum of Natural History, and Princeton University. It is hoped that these studies, in connection with the extensive collections now being made, will make possible a complete discussion of the flora within a few years. No effort will here be made to present a full list of the species represented in the Mascall flora. The following annotated list includes only those species which are of particular geologic interest, inasmuch as they have been reported elsewhere, and those species represented by a considerable number of well-preserved specimens, and therefore of biologic value.

*Ginkgo adiantoides* (Unger) Heer. Only fragmentary material of this genus has been available until recently, when several specimens have been found at the White Hills and other nearby localities.

*Sequoia langsdorfii* (Brgt.) Heer. It seems probable that this species will be made to include *Sequoia angustifolia* Lesq. and *Taxodium distichum miocenum* Heer, since the differences of all three are slight and of an order of those occurring on single trees of the closely related living redwood, *Sequoia sempervirens.*

*Libocedrus sp.* The presence of this genus is indicated by several foliage twigs and by a cone. There are also a number of seeds which may be referable to *Libocedrus.* Specimens previously referred to *Thuites* sp. and certain of those referred to *Glyptostrobus ungeri* may be more properly considered to be *Libocedrus.*

*Populus lindgreni* Kn.

*Salix varians* Göpp.

*Salix angusta* Al. Br.

*Juglans oregoniana* Lesq. In addition to the numerous specimens, properly referred to this species, there are others formerly named as *Salix mixta* and *Rhus bendirei* which appear to be referable to it.

*Carpinus grandis* Ung.

*Alnus sp.* A single specimen of *Alnus* has been called *Alnus kefersteinii* (Gopp) Unger, by Lesquereux, a determination which Knowlton regarded as doubtful. There are several other specimens now available, which more closely resemble the Bridge Creek species, *Alnus carpinoides*, than any other. Since the margins of the Mascall leaves are more conspicuously double serrate, it seems preferable to consider them as possibly representing a distinct species for the present.

*Castanopsis chrysophylloides* Lesq. In the material recently collected are a number of leaf specimens which from their shape, nervation, and texture are clearly referable to *Castanopsis.* Since they are indistinguishable from the living *C. chrysophylla*, they are here referred to Lesquereux's species from the Auriferous Gravels, *C. chrysophylloides.* Certain specimens of *Salix perplexa* are indistinguishable from this species, which is also the case with most or all of the specimens referred to *Sapindus oregonianus.*

*Quercus pseudo-lyrata* Lesq. This abundant species appears to be closely related to *Quercus kelloggii* Newb., the living California black oak, as well as to several species of living eastern oaks. Having in mind the variation in the leaves of these living species, it seems proper to consider *Quercus merriami* and *Quercus ursina* as variants of *Quercus pseudo-lyrata.*

*Quercus duriuscula* Kn. Originally represented by a single specimen, this species has recently been found to be fairly common. Certain specimens closely resemble *Q. columbiana* Chaney of the Eagle Creek flora of the Columbia River Gorge.

*Quercus horniana* Lesq.

*Ulmus californica* Lesq. This specimen was included by Knowlton with doubt.[1] Its relation to other Tertiary members of the genus has not been carefully worked out, but a considerable number of specimens seem to be of the *californica* type.

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[1] Knowlton, op. cit., p. 55.

*Berberis? gigantea* Kn.
*Liquidamber pachyphyllum* Kn.
*Umbellularia* sp. A considerable number of the specimens which have been described as *Salix pseudo-argentea* and *S. dayana* appear to be closely related to the living California laurel, *Umbellularia californica*, and they are here referred to this genus.
*Platanus dissecta* Lesq.
*Cratagus imparilis* Kn.
*Celastrus confluens* Kn.
*Acer bendirei* Lesq. The correctness of the reference of this form to *Acer* has been questioned by the writer in a previous paper.[1] While there can be no doubt that certain of the type specimens of *Acer bendirei* as described by Lesquereux are *Platanus*, there is still some question as to whether all of them are referable to that genus. Two species of *Acer* are indicated by the two types of seeds found in the Mascall shale; one of these may be related to the leaf species listed below as *Acer* cf. *glabrum;* the other suggests the presence in the Mascall flora of a second leaf species, which may be *Acer bendirei.* While *Acer* and *Platanus* are not closely related genera, it is difficult to distinguish between their leaves in some cases. Pending the working out of satisfactory criteria for separating them, *Acer bendirei* will be retained in the list of species, together with *Platanus dissecta,* to which certain if not all of the leaves of *Acer bendirei* can be properly referred
*Acer* cf. *glabrum.*
*Acer oregonianum* Kn.
*Acer gigas* Kn. This and the preceding species are based on impressions of the winged seeds, and from their difference in size there can be little doubt that they represent two species.
*Aesculus simulata* Kn.
*Grewia crenata* (Unger) Heer.

In his discussion of the age of the Mascall formation,[2] Knowlton has given table 1, showing the distribution of the 24 Mascall species which are found outside of the John Day Basin.

Table 1 shows that 18 species occur in the Miocene and a like number in the Eocene at horizons ranging from the Fort Union to the Bridge Creek.[3] Knowlton concludes as follows:[4]

"If dependence were placed exclusively on the distribution of the above-mentioned forms in fixing the age of these beds the tendency would be to regard them as not younger than Lower Miocene, or even possibly as old as the Upper Eocene, but when we take into account the affinities and relationships of the forty or more named species that are confined to these beds, the preponderance of evidence would seem to relegate them to an age as young as the upper Miocene."

Knowlton's reference of the Mascall flora to the Middle or Upper Miocene has been in complete accord with the idea of Merriam and Sinclair, based on their study of the fossil vertebrates of the Mascall formation.[5] Inasmuch, however, as the plant-bearing beds lie 16 miles up the river from the locality on the Mascall ranch from which

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[1] Flora of the Payette Formation. Am. Jour. Sci., vol. 4, p. 219.
[2] F. H. Knowlton, op. cit., p. 107.
[3] The Bridge Creek flora is considered by the writer to be of Upper Oligocene rather than Upper Eocene age.
[4] U. S. Geol. Surv. Bull. 204, p. 108.
[5] Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, No. 11, p. 197.

TABLE 1.—*Extralimital distribution of fossil plants from Van Horn's ranch and vicinity.*

| Species. | Fort Union. | Eocene in general. | Green River. | Eocene of Alaska. | Miocene. | Remarks. |
|---|---|---|---|---|---|---|
| Sequoia langsdorfii | × | × | × | × | × | Upper Cretaceous. |
| Sequoia angustifolia | ...... | ........ | ×? | × | × | |
| Glyptostrobus ungeri | ...... | ........ | × | ×? | × | |
| Taxodium distichum miocenum | × | × | ...... | ........ | × | |
| Phragmites oeningensis | ...... | ........ | ...... | ........ | ...... | Laramie to Pliocene. |
| Populus lindgreni | ...... | ........ | ...... | ........ | × | |
| Salix ræana? | ...... | ........ | ...... | × | × | |
| Salix varians | ...... | ........ | ...... | × | ...... | |
| Salix angusta | ...... | ........ | ...... | ........ | ...... | Whole Tertiary. |
| Salix amygdalæfolia | ...... | ........ | × | ........ | × | |
| Juglans oregoniana | ...... | ........ | ...... | ........ | × | |
| Carpinus grandis? | ...... | × | × | ........ | × | |
| Alnus kefersteinii? | ...... | ........ | ...... | × | × | |
| Ulmus plurinervia | ...... | ........ | ...... | × | ...... | |
| Ulmus californica | ...... | ........ | ...... | ........ | × | |
| Artocarpus californica? | ...... | ........ | ...... | ........ | × | |
| Magnolia lanceolata | ...... | ........ | ...... | ........ | × | |
| Magnolia inglefieldi | ...... | ........ | ×? | ........ | ...... | Lassen County, Calif. |
| Platanus nobilis? | × | ×? | ...... | ........ | ...... | |
| Platanus aceroides? | ...... | ........ | ...... | ........ | ...... | Laramie to Miocene. |
| Acer bendirei | ...... | ........ | ...... | ........ | × | |
| Sapindus obtusifolius | × | | | | | |
| Sapindus angustifolius? | ...... | × | × | ........ | × | |
| Grewia crenata | ×? | × | ...... | ........ | ...... | Bridge Creek. |

most of the vertebrate fossils have been secured, there has been some doubt as to the stratigraphic relations of the two deposits. To be sure, the Mascall formation appears to be traceable continuously up stream from the Mascall ranch to Van Horn's ranch, and the same diatomaceous layers associated with gray sands are found at the base of each section. But in the case of terrestrial deposits of this sort, the only certain basis for correlation is the palaeontologic relation of the two localities. This has not been demonstrated until the finding within recent years of a small flora immediately overlying the Columbia lava on Rock Creek at a short distance from the type-vertebrate locality. This flora is contained in deposits which appear to have had a somewhat different origin than the shales at the typical plant localities, and is made up of fewer and less well-preserved species. Its two well-defined species, *Sequoia langsdorfii* and *Ulmus californica*, are among the common Mascall flora forms, and in addition there are three more, *Typha* sp., *Fraxinus* sp., and *Carpites* sp., which occur also at the Van Horn's ranch locality, but which have not been listed for that locality because of their doubtful character. In view of the fact that all of its species are present at the type-plant locality, the Rock Creek flora may be considered as closely related to the typical Mascall flora; and the position of the shales containing the Rock

Creek flora, below the Mascall fauna, appears to furnish strong evidence of the Middle Miocene age of the flora both at Rock Creek and at the Van Horn's and White Hills localities.


FIG. 1.

The geographic distribution of the floras containing plants of the Mascall type is shown in the accompanying map. The localities nearest to the John Day Basin are in the Blue Mountains of Oregon, near the towns of Austin and Tipton,[1] a distance of 45 miles from

[1] There is an appended list of the localities discussed in this paper, with complete descriptions of their location.

the Van Horn's ranch locality. Leaf impressions occur here in a diatomaceous shale which is not distinguishable from that in the John Day Basin, and appears to have the same stratigraphic position, with basalt flows below and with rhyolite of the Rattlesnake type above and intruding it. Of the total of 19 species, 13 are included in the list from the Van Horn's ranch and White Hills localities, including *Sequoia langsdorfii*, *Umbellularia* sp., *Quercus pseudo-lyrata*, *Platanus dissecta*, and *Aesculus simulata*, which are among the most characteristic species in each flora. In addition there are 6 species which have not been recorded from the John Day Basin, but most of which are listed for some of the other localities which are discussed below. In the following list of species, those which are common to the John Day Mascall are marked with an asterisk, a practice which is followed in all of the other locality lists.[1]

| | | |
|---|---|---|
| Acer cf. circinatum | Cornus ovalis | *Quercus horniana |
| *Acer gigas | Pinus cf. attenuata | *Quercus pseudo-lyrata |
| *Acer cf. glabrum | *Platanus dissecta | *Umbellularia sp. |
| *Aesculus simulata | *Populus lindgreni | *Salix varians |
| *Alnus sp. | Quercus consimilis | *Sequoia langsdorfii |
| *Berberis? gigantea | Arbutus sp. | *Ulmus californica |
| Cercocarpus antiquus | | |

In his paper on the fossil plants of the John Day Basin, Knowlton has pointed out the close resemblance of the flora of the Ellensburg formation of Washington to the Mascall flora.[2] The following list of Ellensburg species, somewhat revised, is taken from Knowlton's report in the Ellensburg Folio.[3]

| | | |
|---|---|---|
| *Alnus sp. | *Populus lindgreni | *Salix varians |
| Magnolia dayana | *Quercus pseudo-lyrata | *Ulmus californica. |
| *Umbellularia, sp. | *Platanus dissecta | |

All but two of these are among the more abundant of the Mascall species; *Populus lindgreni* also occurs in the Mascall, but is not common.

In 1920, a small collection of leaf impressions was made by the writer near Spokane, Washington. The abundance of the leaves of *Quercus pseudo-lyrata* suggested the relationship of these deposits to the Mascall formation. Subsequently, Knowlton has worked over extensive collections from this region, and the results of his work are soon to be published. According to Bryan and Pardee, who are to present a statement of the geology to accompany Knowlton's report, the Latah formation in which the leaves occur represents the sedimentary accumulations laid down during the outflow of the lavas farther to the west. If these lavas are the equivalent of the Columbia lavas, the Miocene age of the Latah formation is thereby in-

[1] In the U. S. National Museum there are two small collections made by Hewitt, of the U. S. Geological Survey at points within a few miles of Austin. The matrix is like that at Austin, and all of the 10 or more species are represented in the collections from Austin and Tipton.

[2] U. S. Geol. Surv., Bull. 204, pp. 109–110.

[3] U. S. Geol. Surv., Ellensburg Folio, p. 3.

dicated. In any case, a close similarity of the Latah to the Mascall flora is apparent.

The resemblance of the Payette flora to the Mascall has previously been pointed out by the writer.[1] The following list indicates its relation to the Mascall.

*Acer gigas
*Aesculus simulata
*Juglans oregoniana
Laurus princeps
Libocedrus sp.
*Odostemon simplex
Pinus knowltoni
*Platanus dissecta
*Populus lindgreni
Quercus clarnoensis
*Quercus consimilis
*Salix angusta
*Umbellularia sp.
*Castanopsis chrysophylloides
*Sequoia langsdorfii
*Ulmus californica
Ulmus sp.

Of the 6 species not occurring in the John Day Mascall, 3 are recorded from other related localities in this paper, and 5 are among the common forms of the Bridge Creek and other Upper Oligocene floras of the West. On the basis of these relations the Payette flora can hardly be considered to be younger than Middle or Upper Miocene. The stratigraphic position of the Payette formation, overlying what appears to be an eastward extension of the Columbia lavas, is in accord with this age reference, as is the vertebrate evidence.[2]

There is an extensive exposure of diatomaceous shale bearing leaf impressions along Trout Creek, in southeastern Oregon, 160 miles to the South of Austin. It reaches a thickness of 100 feet or more, and is overlaid by basaltic lavas. Material was collected here in 1907 by Mendenhall, of the U. S. Geological Survey, and the age of the beds was determined by Knowlton as Upper Eocene, largely on the basis of the presence of *Quercus consimilis*, one of the characteristic species of the Bridge Creek flora of the John Day Basin. More extensive collections have recently been made by Furlong and Stock, of the University of California, raising the total number of species to 9. Of these, *Quercus consimilis* is the only species not found in the Mascall formation at the type locality. Its presence in the Blue Mountain collections and at other localities which furnish a typical Mascall flora indicates that its association with a group of typical Mascall species at Trout Creek is not abnormal, and that it is a species which ranges well above the Bridge Creek horizon. A small vertebrate fauna collected by Stock and Furlong in the sedimentary beds below the diatomaceous shale has been studied by them in a preliminary way, and it appears to be of Oligocene or more probably of Miocene age. The list of plants is as follows:

*Acer gigas
*Acer oregonianum
*Alnus sp.
*Celastrus confluens
*Crataegus imparilis
*Libocedrus sp.
*Platanus dissecta
Quercus consimilis
*Umbellularia sp.

In northwestern Nevada, at Forty-nine Camp, the occurrence of leaf-bearing diatomaceous shales overlaid by basaltic lavas

[1] Am. Jour. Sci., vol. 4, 1922, pp. 214–222.
[2] Op. cit., p. 220.

appears to be identical with that at Trout Creek, some 90 miles to the east and north. The collections made here during the past two years by the writer and R. J. Russell comprise 13 species, of which 9 are present at the type locality in the John Day Basin, and all of the remainder are found at other related localities discussed in this paper:

| | | |
|---|---|---|
| Acer bolanderi | *Juglans oregoniana | *Quercus pseudo-lyrata |
| *Acer cf. glabrum | *Platanus dissecta | Rhus myricaefolia |
| *Acer oregonianum | Quercus consimilis | *Umbellularia sp. |
| *Aesculus simulata | Arbutus sp. | *Ulmus californica |
| *Celastrus confluens | | |

On the basis of this list, which is made up almost entirely of Mascall species, including most of the characteristic forms, the Forty-nine Camp flora can be referred without question to the Miocene. A vertebrate fauna has been collected by Stock near Alturas, in tuffs overlying a shale which resembles the leaf-bearing formation at Forty-nine Camp. The fauna is made up of types which appear not to be older than Pliocene, and for this reason there has been a suggestion that the flora at Forty-nine Camp might be younger than the Miocene. A small flora has been collected by Miss Annie M. Alexander and Miss Louise Kellogg from a point near Stock's vertebrate locality and at the same horizon, which indicates that his fauna is probably not of the same age as the flora from Forty-nine Camp. This flora from the Alturas locality is made up of only two species so far as now known, neither of which occurs in the Mascall. The close relation of these two species to living forms of poplar and willow suggests that they are younger than the Miocene, and is wholly consistent with the suggestion of Pliocene age for the vertebrate remains found with them. So far as now known, there is no reason for correlating the leaf-bearing shales at Forty-nine Camp with the tuffs containing vertebrate remains near Alturas.

A small collection has been made by R. J. Russell on the Pitt River in California, some 60 miles west of Forty-nine Camp, in diatomaceous shales. Of the 6 species represented, all are typical Mascall forms except *Quercus convexa,* which is one of the most characteristic species of the Auriferous Gravels at Table Mountain, California.

| | | |
|---|---|---|
| *Aesculus simulata | *Juglans oregoniana | *Sequoia langsdorfii |
| Alnus sp. | Quercus convexa | *Umbellularia sp. |

The problem of the age of the floras of the Auriferous Gravels of the Sierra Nevada in California has been complicated by the fact that few of the plant species have been found elsewhere, and by the grouping together of collections of plants from what appear to represent several horizons. As originally described by Lesquereux,[1] the floras

[1] Leo Lesquereux, Report on the fossil plants of the auriferous gravel deposits of the Sierra Nevada.

of the Auriferous Gravels were referred to the Pliocene on the basis of the close resemblance of many of the species to those now living. Subsequently, Knowlton pointed out their Miocene affinities,[1] and there is little reason to question this age so far as the flora from Table Mountain, Tuolumne County, is concerned, although the floras from Chalk Bluffs and Independence Hill, to the north, may probably be somewhat older. A new plant locality at Table Mountain was discovered by Matthes, of the U. S. Geological Survey in 1921, from which the writer made rather extensive collections during the following year. The leaf impressions occur in a layer of andesite tuff, ranging texturally from a fine clay to a medium sand. This layer is about 15 feet thick, and rests upon gravels made up largely of granite pebbles, or upon the granite bedrock itself.

| | | |
|---|---|---|
| Acer bolanderi | Persea pseudo-argentea | Rhus typhinoides |
| Cercocarpus antiquus | *Platanus dissecta | *Salix angusta |
| Cornus ovalis | Quercus convexa | *Umbellularia sp. |
| Ficus microphylla | Arbutus sp. | *Ulmus californica |
| Magnolia californica | Rhus myricæfolia | |

While only 4 species have been recorded from the John Day Mascall, 3 of these, *Platanus dissecta, Umbellularia* sp., and *Ulmus californica,* are among the most characteristic species. In addition, 6 of the Table Mountain species have been found at the Blue Mountain localities, and a like number occur at Forty-nine Camp. Of the total of 14 species, 10 are present in localities in Washington, Oregon, and Nevada which furnish the typical Mascall flora, including several of the most characteristic species. In addition, there are 2 species, *Platanus dissecta* and *Persea pseudo-carolinensis,* which occur in the San Pablo flora of California. Altogether there are 12 of the 14 species which are found in beds commonly considered to be in the Miocene of the West.

The recent finding of two teeth of *Hipparion* in the gravels below the leaf-bearing tuffs at Table Mountain has suggested the possibility that the deposits here may be of Lower Pliocene age.[2] There is some difference of opinion among vertebrate palaeontologists as to whether *Hipparion* may not range down into the Miocene.[3] The association of these teeth with a flora that appears to be Miocene suggests that *Hipparion* may occur in the Middle or Upper Miocene of California.

At this point it may be mentioned that almost nothing is known of the Pliocene floras of the West. The finding of a small flora of probable Pliocene age near Alturas, California, has been noted above. Hannibal has published a paper on a Pliocene flora from the Coast Ranges of California,[4] but the species listed by him are many of them

[1] F. H. Knowlton, U. S. Geol. Surv., Prof. Paper 73. 1911.
[2] John C. Merriam, Year Book Carnegie Inst. Wash., No. 21, p. 400. 1922.
[3] See W. D. Matthew, Correlation of the Tertiary Formations of the Great Plains, Bull. G. S. A. vol. 35, pp. 752–753. 1924.
[4] Harold Hannibal, Bull. Torrey Bot. Club, vol. 38, pp. 329–342, pl. 15, 1911.

chaparral forms, and are unrelated to the Miocene and older floras of the West. A small collection of plants has recently been made by the writer in the Sonoma tuffs near Santa Rosa, California, a formation which has been referred to the Pliocene on the basis of the vertebrates which have been found in it.[1] The flora includes 7 species, the most abundant of which is a species of *Platanus* resembling *P. racemosa*, the sycamore now living on the Pacific Coast, in having a typically entire margin. The living members of the genus occurring in the eastern United States and eastern Asia have typically serrate margins, a character which is shared by the abundant and wide-ranging Miocene species, *Platanus dissecta.* A study of the ranges of the fossil and living species of *Platanus* from the Miocene to the present indicates that the serrate type may be more primitive, and that the entire *racemosa* type may have developed from it, first appearing in the Pliocene of California and continuing down to the present with a distribution restricted to the Western United States. If the *racemosa* type of leaf can be shown to be the characteristic representative of the genus from the Pliocene to the present in California, the presence of *Platanus dissecta* in the tuffs at Tuolumne Table Mountain is strongly suggestive of their pre-Pliocene age. At any rate, *Platanus dissecta* is not known to occur in beds certainly younger than Miocene, either in California or elsewhere in the West.

The San Pablo formation of the Coast Ranges of California contains a flora referred to the Miocene by Knowlton.[2] The leaf impressions occur in andesitic clays and sands interbedded with marine sediments. 22 species of plants have been recorded from the San Pablo in the region around Mount Diablo and Corral Hollow, of which *Platanus dissecta* and *Sequoia langsdorfii* are characteristic Mascall forms and several others appear to be identical with Mascall forms, although listed under different names. There are also at least two species in common with the flora from Tuolumne Table Mountain. The available evidence of the plants seems therefore to indicate that the San Pablo and the Mascall formations are of about the same age. The age of the invertebrate fauna which occurs in the marine strata associated with the plant-bearing layers has been discussed by Clark,[3] who concludes that it is Upper Miocene or Lower Pliocene in age, more probably the former.

In a recently published paper, Louderback[4] presents the evidence for correlating the San Pablo with the Sierran andesites. In addition

[1] Roy E. Dickerson, Tertiary and Quaternary history of the Petaluma, Point Reyes, and Santa Rosa Quadrangles. Proc. Calif. Acad. Sci., 4th ser., vol. 11, No. 19, pp. 556–559.

[2] F. H. Knowlton, Flora of the Auriferous Gravels of California. U. S. Geol. Surv., Prof. Paper 73, 1911, p. 63.

[3] B. L. Clark, Fauna of the San Pablo group of Middle California, Univ. Calif. Publ., Bull. Dept. Geol., vol. 8, 1915, pp. 385–572.

[4] George D. Louderback, Period of scarp production in the Great Basin, Univ. Calif. Publ., Bull. Dept. Geol., vol. 15, No. 1, 1924, pp. 1–44.

to reviewing the palaeontologic relationships, he develops the idea that the andesitic gravels and sandstones of the San Pablo represent the material carried from the areas of Sierran volcanic activity and deposited in the San Pablo sea. This suggestion of the contemporaneity of the Sierra andesites and the San Pablo formation is in full accord with the floral evidence as already outlined. It is therefore possible not only to relate the San Pablo formation of the Coast Ranges to the Sierran andesites, notably those at Tuolumne Table Mountain, but to suggest their probable contemporaneity with the Mascall formation and other related deposits of the Great Basin. The final establishment of such relationship is of utmost importance in the correlating of the Coast Ranges formations with their marine faunas, and the Great Basin deposits containing terrestrial faunas and floras.

The floras on the east side of the Sierra Nevada are too incompletely known to make possible any certain statement as to their relation to the Mascall flora. The Truckee beds near Verdi [1] appear to contain a flora similar to that of the Esmeralda beds, [2] but no critical species from either flora have been recorded elsewhere. Rather extensive collections have been made at the Verdi locality by the writer within recent years, and there is some reason for believing that this flora is not younger than the Mascall. It is possible that the difference between the Verdi and Mascall floras is the result of two unlike habitats, in which differences of altitude and climate have produced two dissimilar floras which are essentially contemporaneous. A large amount of further work must be done before the relations of these floras can be satisfactorily established. The flora from Elko, Nevada, is made up largely of *Sequoia langsdorfii* (of the *angustifolia* type), and from the evidence at hand may be of the same age as the Mascall flora or possibly as old as the Bridge Creek, which is now referred to the Upper Oligocene.

Table 2 shows the distribution of the species in the localities above discussed, with the exception of the Latah formation, for which a complete list is not now available, and of the San Pablo, which is omitted from this part of the discussion because of its relatively slight numerical relation to the Mascall flora proper. *Umbellularia* sp. is the most wide-ranging species, occurring in all of the 8 localities; *Platanus* is nearly as widespread, with representation in 7 localities; and *Ulmus californica* is present in 6; these 3 species range into all of the five States as well. *Sequoia langsdorfii*, *Aesculus simulata*, and *Alnus* sp. are represented in 5 localities each, and *Populus lindgreni*,

[1] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 9, 1916, p. 167.

[2] F. H. Knowlton, Fossil plants of the Esmeralda formation, U. S. Geol. Surv., 21st Ann. Rept., pt. 2, pp. 209–220, 1900.

TABLE 2.

| Species. | Mascall Flora. | | | | | | | | Eocene. | | | Oligocene. | | | | | Miocene | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | John Day Valley, Oregon. | Blue Mountains, Oregon. | Ellensburg, Washington. | Payette, Idaho. | Trout Creek, Oregon. | Forty-nine Camp, Nevada. | Pitt River, California. | Tuolumne Table Mt., Calif. | Fort Union. | Kenai. | Green River. | Bridge Creek. | Eagle Creek. | Oligocene of Brit. Columbia. | Chalk Bluffs. | Independence Hill. | Florissant. | Yellowstone Park. | Esmeralda. | British Columbia. | Calvert. |
| Ginkgo adiantoides | × | | | | | | | | × | × | | | × | × | | | | | | | |
| Sequoia langsdorfii | × | × | | × | | | × | | × | × | | × | | | | | × | | | | |
| Libocedrus sp. | × | | | × | × | | | | | | | | | | | | | | | | |
| Populus lindgreni | × | × | × | × | | | | | | | | | | | | | | | | | |
| Salix varians | × | × | × | | | | | | | × | | | | | | | | × | | | |
| Salix angusta | × | | | × | | | | × | | | × | | | | | | | × | × | | |
| Umbellularia sp. | × | × | × | × | × | × | × | × | | | | | | | | | | | | | |
| Juglans oregoniana | × | | | × | | × | × | | | | | | | | | | | | | | |
| Carpinus grandis | × | | | | | | | | | × | | × | | | | | × | | | | × |
| Alnus sp. | × | × | × | | × | | × | | | | | | | | | | | | | | |
| Quercus pseudo-lyrata | × | × | × | | | × | | | | | | | × | | | | | | | | |
| Quercus duriuscula | × | | | | | | | | | | | | | | | | | | | | |
| Quercus horniana | × | × | | | | | | | | | | | | | | | | | | | |
| Ulmus californica | × | × | × | × | | × | | × | | | | | | | × | × | | | | | |
| Berberis? gigantea | × | × | | | | | | | | | | | | | | | | | | | |
| Liquidambar pachyphyllum | × | | | | | | | | | | | | × | | | | | | | | |
| Platanus dissecta | × | × | × | × | × | × | | × | | | | | | | × | | | | | | |
| Cratægus imparilis | × | | | | × | | | | | | | | | | | | | | | | |
| Celastrus confluens | × | | | | × | × | | | | | | | | | | | | | | | |
| Acer bendirei | × | | | | | | | | | | | | | | | | | | | × | |
| Acer oregonianum | × | | | | × | × | | | | | | | | | | | | | | | |
| Ficus mensæ | | | | | | | | × | | | | | | | | | | | | | |
| Acer gigas | × | × | | × | × | | | | | | | | | | | | | | | | |
| Aesculus simulata | × | × | | × | | × | × | | | | | | | | | | | | | | |
| Castanopsis chrysophylloides | × | | | × | | | | | | | | | | | | | | | | | |
| Grewia crenata | × | | | | | | | | × | | | × | | × | | | | | | | |
| Acer cf. glabrum | × | × | | | | × | | | | | | | | | | | | | | | |
| Quercus consimilis | | × | | × | × | × | | | | | | × | | | | | | | | | |
| Acer. cf. circinatum | | × | | | | | | | | | | | | | | | | | | | |
| Pinus cf. attenuata | | × | | | | | | | | | | | | | | | | | | | |
| Cornus ovalis | | × | | | | | | × | | | | | | | | × | | | | | |
| Cercocarpus antiquus | | × | | | | | | × | | | | | | | | × | | | | | |
| Arbutus sp. | | × | | | | × | | × | | | | | | | | × | | | | | |
| Rhus typhinoides | | | | | | | | × | | | | | | | | | | | | | |
| Magnolia dayana | | | × | | | | | | | | | | | | × | × | | | | | |
| Laurus princeps | | | | × | | | | | | | | | | | | | | | | | |
| Odostemon simplex | | | | × | | | | | | | | × | | | | | | | | | |
| Pinus knowltoni | | | | × | | | | | | | | | × | | | | | | | | |
| Quercus berryi | | | | × | | | | | | | | | × | | | | | | | × | |
| Ulmus speciosa | | | | × | | | | | | | | × | × | | | | | | | | |
| Acer bolanderi | | | | | | × | | × | | | | | × | | | | | | | | |
| Rhus myricæfolia | | | | | | × | | × | | | | | | | × | × | | | | | |
| Quercus convexa | | | | | | | × | × | | | | | | | | × | | | | | |
| Magnolia californica | | | | | | | | × | | | | | | | × | × | | × | | | |
| Persea pseudo-carolinensis | | | | | | | | × | | | | | | | | × | | × | | | |
| Total | 26 | 19 | 8 | 17 | 9 | 13 | 6 | 14 | 3 | 4 | 1 | 7 | 7 | 2 | 5 | 9 | 2 | 4 | 1 | 3 | 1 |

*Juglans oregoniana, Quercus pseudo-lyrata, Acer gigas,* and *Quercus consimilis* are represented in 4. These 11 species are not only the most widely distributed of the flora, but they are in most cases also the most abundant in the individual floras; especially is this true of *Umbellularia* sp., *Platanus dissecta, Ulmus californica, Quercus pseudo-lyrata,* and *Quercus consimilis.*

There is a considerable degree of unity to be observed in the floras from most of the 8 localities. Thus it may be seen, as shown in table 3, that of 26 forms listed from the John Day Basin, 20 are represented in at least one other locality, and 10 are represented in half of the localities, while of 19 forms listed from the Blue Mountains, all but 2 have been recorded from at least one other locality, and 10 have been recorded in four or more localities.

Table 3.

| Locality. | Total number of species recorded. | Species occurring in at least one other locality. | | Species occurring in at least half the localities. | |
|---|---|---|---|---|---|
| | | No. of species. | Per cent of total. | No. of species. | Per cent of total. |
| John Day Basin | 26 | 20 | 76.9 | 10 | 38.5 |
| Blue Mountains | 19 | 17 | 89.5 | 10 | 52.6 |
| Ellensburg | 8 | 7 | 87.5 | 6 | 75 |
| Payette | 17 | 12 | 70.6 | 9 | 52.9 |
| Trout Creek | 9 | 9 | 100 | 5 | 55.5 |
| Forty-nine Camp | 13 | 13 | 100 | 7 | 53.8 |
| Pitt River | 6 | 6 | 100 | 5 | 83.3 |
| Table Mountain | 14 | 11 | 78.6 | 3 | 21.4 |

On an average, slightly more than seven-eighths of each flora has representation in the flora from at least one other locality, while over one-half of each flora is found in the floras from one-half of the other localities. A thorough taxonomic revision of the lists as given in table 3 would greatly increase the relationships between the floras from different localities. For example, *Pinus* cf. *attenuata* is probably the cone of the leaf species, *Pinus knowltoni; Quercus berryi* may not be distinguishable from *Quercus consimilis;* and the 4 leaf species of *Acer* listed probably do not represent more than two actual species. If such combinations are ultimately made, the unity of the flora will become even more apparent, but even on its present basis the relationship between the lists of species from the eight localities is well enough established to indicate that the Mascall type of forest formation was widely distributed during that part of the Tertiary following the outpouring of the Columbia lavas.

Table 2 also shows the occurrence of the Mascall flora at other localities and horizons in North America. 25 of the total of 45 species

have an outside distribution, of which 6 have been reported in the Eocene, 12 in the Oligocene, and 17 in the Miocene, if this system is taken to include the Auriferous Gravels of Nevada and Placer Counties, California. All 6 of the Eocene species are long-lived, having been reported elsewhere throughout most of the Tertiary, as shown in the table. Unfortunately this is also true, though to a somewhat less extent, of the Oligocene and Miocene species. The value of the occurrence table is further diminished by the absence of any considerable record of the character and distribution of the Pliocene floras of the West, since if it were known this might show a considerable number of Mascall species common also to the Pliocene. There is a further difficulty in the uncertain status of the age of the floras from the Auriferous Gravels at Chalk Bluffs and Independence Hill. Originally referred to the Pliocene by Lesquereux,[1] these floras have later been considered to be of Miocene age by Knowlton,[2] and within late years the suggestion of their reference to the Eocene has found acceptance because of the association of certain Auriferous Gravels plants with an Eocene invertebrate fauna in southwestern Oregon.[3] In view of the fact that the plant material is so poorly preserved in this latter situation as to make its positive determination impossible except in the case of 3 species, the writer is in full agreement with Knowlton in his opinion that the Chalk Bluffs and Independence Hill floras may best be referred to the Miocene, though it is possible that further work will show their closer relation to the Oligocene. The correctness of their reference to the Miocene is further indicated by the relationship of these Auriferous Gravels floras to the Mascall assemblage as here described. Obviously this relationship can not be used to prove the Miocene age of either flora, except as evidence is furnished to indicate the Miocene age of the Mascall plants on other grounds. In view of the fact that floras which may be supposed to be younger than the Mascall are at the present time largely unknown, and that practically all of the Mascall species reported from horizons of known age are geologically long-lived, any effort to determine the age of the Mascall flora from the plants themselves must be based not on a consideration of the individual species but on the plant community as a whole.

As a means of best considering the relations of the Mascall flora in this way, it is instructive to compare it with the oak-madroño forest, a closely related plant community now living in California. This forest has been studied by Cooper.[4] whose list of dominant species,

[1] Mus. Comp. Zool. Mem., vol. 6, No. 2, 1878, pp. 38–55.
[2] U. S. Geol. Surv., Prof. Paper 73, 1911, pp. 57–64.
[3] U. S. Geol. Surv. Bull. 353, 1908, p. 77.
[4] William S. Cooper, The broad-sclerophyll vegetation of California, Carnegie Inst. Wash. Pub. No. 319, 1922.

together with the corresponding Mascall forms, is shown in the following table.

TABLE 4.—*Dominant species of the oak-madroño forest and the corresponding species in the Mascall.*

| Oak-madroño forest. | Mascall flora. |
|---|---|
| Myrica californica | |
| Castanopsis chrysophylla | Castanopsis chrysophylloides. |
| Quercus agrifolia | Quercus convexa. |
| Quercus chrysolepsis | |
| Quercus engelmanni | |
| Quercus wislizeni | |
| Quercus kelloggii | Quercus pseudo-lyrata. |
| Quercus lobata | Quercus duriuscula. |
| Pasania densiflora[1] | Quercus consimilis. |
| Umbellularia californica | Umbellularia sp. |
| Arbutus menziesii | Arbutus sp. |
| Acer macrophyllum | Aesculus simulata. |

Nine of the thirteen dominants of this forest of to-day are represented by related species in the Mascall flora. As a matter of fact, four species of the modern oaks, *Quercus chrysolepis*, *Q. agrifolia*, *Q. engelmanni*, and *Q. wislizeni*, are all of the evergreen type, and in many cases can be distinguished with difficulty on the basis of the leaves alone. This being the case, the Mascall species of evergreen oak, *Quercus convexa*, may be considered to represent more than one of the modern species, and possibly all four of them. *Myrica* alone is absent in the Mascall flora, which is not surprising in view of the high degree of sensitivity of the living *M. californica* to variations in humidity.

The oak-madroño forest is characteristic of the lower altitudes in the northern Coast Ranges at the present time, and one locality is cited by Cooper in the valley of the South Fork of the Eel River in Humboldt County, California, where the following species are dominant: *Pasania densiflora*, *Quercus kelloggii*, *Q. chrysolepis*, *Q. garryana*, *Arbutus menziesii*, *Umbellularia californica*, *Aesculus californica*, *Acer macrophyllum*, and *Pseudotsuga*. Of these, only the last is unrepresented by a closely related species in the Mascall flora, and it may well have been present without leaving a conspicuous fossil record.[2]

The list of species associated with the dominants of this forest brings out a further relationship between it and the Mascall flora. At a point on the Eel River near that described by Cooper, the writer has noted in association with the typical oak-madroño community

[1] Some botanists recognize the intermediate character of this form between the oaks and chestnuts and give it this generic designation.

[2] See, A comparative study of the Bridge Creek flora and the modern redwood forest. Carnegie Inst. Wash. Pub. No. 349, p. 3, 1924,

various species which have closely related fossil equivalents in the Mascall flora. *Pinus ponderosa* in the living forest is closely similar to *Pinus knowltoni* in the Mascall, *Salix sitchensis* corresponds to the fossil *Salix varians*, *Populus trichocarpa* to the fossil *Populus lindgreni*, *Alnus rubra* to the fossil *Alnus* sp., *Crataegus rivularis* to the fossil *Crataegus imparilis*, and *Fraxinus oregona* to a fossil species represented by seeds and not yet given a specific name. This community is characteristic of the border of the redwood forest here and elsewhere in the Redwood Belt. It also bears the same relation to the montane forest of the Sierra Nevada and the Cascades.

At Jasper Ridge, 4 miles southwest of Palo Alto, California, where a detailed study of the plant communities has been made by Cooper,[1] the presence of redwoods (*Sequoia sempervirens*) in association with the oak-madroño forest is particularly significant in the present discussion. Recent studies have been made here by the writer with the assistance of Herbert L. Mason, of the University of California. The oak-madroño forest occupies the lower slopes of Jasper Ridge and is particularly well developed along the course of San Francisquito Creek, where it flows close to the north side of the Ridge. The common trees are listed in table 5, together with their Mascall equivalents.

TABLE 5.—*Characteristic trees at Jasper Ridge and their Mascall equivalents.*

| Jasper Ridge. | Mascall flora. |
|---|---|
| Sequoia sempervirens | Sequoia langsdorfii. |
| Salix laevigata | Salix varians. |
| Salix lasiolepis | Salix varians. |
| Populus trichocarpa | Populus lindgreni. |
| Alnus rhombifolia | Alnus sp. |
| Quercus kelloggii | Quercus pseudo-lyrata. |
| Quercus agrifolia | Quercus convexa. |
| Quercus lobata | Quercus duriuscula. |
| Umbellularia californica | Umbellularia sp. |
| Arbutus menziesii | Arbutus sp. |
| Acer macrophyllum | Acer bolanderi. |
| Aesculus californica | Aesculus simulata. |

There is a single tree of *Juglans californica* on the creek border; it may have been introduced, but the presence in the Mascall flora of numerous leaves of a closely related species, *Juglans oregoniana*, suggests that the walnut occurred normally in this association at least during the Tertiary. While the common western sycamore, *Platanus racemosa*, is not present at Jasper Ridge, it is a dominant species in the oak-madroño forest along Stevens Creek, some 12 miles to the southeast. It should be noted that the western sycamore generally occupies a less moist habitat and has a more xero-

[1] Carnegie Inst. Wash. Pub. No. 319, pp. 30–71.

phytic type of leaf than the species living in the eastern United States (*P. occidentalis*) and in Asia (*P. orientalis*), to which the Mascall species, *P. dissecta*, is related. The tanbark oak, *Pasania densiflora*, is a characteristic member of the broad-sclerophyll forest in general, but is lacking at Jasper Ridge. It is abundant, however, in the Santa Cruz Mountains, 2 or 3 miles distant. The corresponding species in the Mascall assemblage is *Quercus consimilis*.

At Jasper Ridge the redwood occurs in small groups along the stream opposite the small canyons made by its tributaries, and in some cases extends up the ravines formed by the tributaries. Although some of the trees appear to be full grown, none of them is as large as those in the typical redwood forest, the largest observed having a diameter at eye-level of less than 5 feet. Their survival in this valley appears to be due in large part to the "leakage" of ocean fog over a saddle in the Santa Cruz Range to the northwest and the regular passage of this fog down the valley. Where redwoods are growing on the edge of the creek, leaf-bearing twigs are abundant in the pools along its course. The leaves of all of the other modern species listed in table 5 were also noted in the stream-bed. The leaves of the shrubs on Jasper Ridge are not as commonly present in the pools along the stream, although several species, including *Ribes californicum*, *Physocarpus capitatus*, *Holodiscus discolor*, *Rhus diversiloba*, and *Cornus pubescens*, were noted there; of these only the last two have corresponding species in the Mascall flora, in which there are two species of *Rhus* listed, *R. myricæfolia* and *R. typhinoides*, and one of *Cornus* (*C. ovalis*). In addition, there is a species of *Cercocarpus*, (*C. antiquus*), which is the equivalent of *Cercocarpus parvifolius*, a characteristic member of the chaparral formation on the upper slopes of Jasper Ridge. The relative scarcity of the leaves of shrubs from the depositional record of to-day is due in part to their distance from the stream, in part to the relatively small number of leaves which grow in a shrub as compared to a tree, and in part to the relatively short distance of the leaf of a shrub above the ground, a situation which reduces its chance of being transported widely by the wind after shedding. As might be anticipated, the record of the Mascall shrubs forms an inconspicuous part of the fossil record.

There is a clearly established resemblance between the oak-madroño forest with its associated redwoods at Jasper Ridge and the assemblage making up the Mascall flora. Every tree of the former has a fossil equivalent in the latter, and at least 3 genera of shrubs are common to each. It is of the utmost importance to note further that of the 11 wide-ranging and abundant Mascall species noted on page 40 of this paper, only one[1] is not included among the

[1] *Acer gigas*, a seed species, is here considered to be the Mascall equivalent of the living *Acer macrophyllum*.

characteristic species in the valley below Jasper Ridge, and in similar situations in the nearby valleys. This species, *Ulmus californica*, has no generic representative living in the West at the present time, which accounts for the absence of its equivalent here; it may be noted, however, that the valley habitat at Jasper Ridge resembles that of the elms in the eastern United States. Such trees as *Quercus agrifolia* and *Q. lobata*, which grow most commonly at a distance from the stream, and the shrubs, including *Cornus pubescens*, *Cerocarpus parvifolius*, and *Rhus diversiloba*, all of which make up an inconspicuous part of the leaf record in San Francisquito Creek, have similarly inconspicuous equivalents in the Mascall flora, in which *Quercus convexa* occurs in only two localities, *Quercus duriuscula* in but one, *Cornus ovalis* in two, and *Rhus typhinoides* in one locality; in addition to having restricted ranges, none of these species is represented by more than a few specimens.

The Mascall flora contains a considerable number of species which have no generic representation in the oak-madroña forest, including such forms as *Libocedrus* sp., and *Odostemon simplex*, of which there are related species in other plant formations in the West to-day; *Ficus mensae*, which has generic representatives in Mexico and Florida; *Carpinus grandis*, *Ulmus californica*, *Liquidambar pachyphyllum*, *Ficus mensae*, *Magnolia dayana* and *M. californica*, and *Persea pseudocarolinensis*, which are found in the eastern United States; and *Ginkgo adiantoides*, *Grewia crenata*, and *Laurus princeps*, which do not occur in North America at the present time. Such differences between Tertiary and modern equivalent forests are to be expected, in view of the apparently wider geographic range of many genera of plants in the past. But in this case they are exaggerated, in the opinion of the writer, by what appear to be incorrect references to several of these genera. As has been previously pointed out,[1] the leaves referred to *Grewia* appear to be more properly referable to *Cercis*; the California redbud, *Cercis occidentalis*, is commonly found associated with the oak-madroño forest at the present time, and the occurrence of its Tertiary equivalent with the Mascall flora seems much more probable than that of *Grewia*, a genus largely tropical and now found in Asia, Africa, and Australia. In any event, there are living species of most of the genera, above noted as absent from the oak-madroño forest formation, which might readily grow in such habitat at the present time, and which may well have been associated with the more typical members of the Mascall assemblage during the Tertiary. In so far as these genera are correctly named, their presence in the Mascall assemblage indicates that it should be placed well down in the Tertiary.

[1] R. W. Chaney, Quantitative studies of the Bridge Creek flora, Am. Jour. Sci. vol. 8, pp. 131–132, 1924.

Having established a close relationship between the Mascall flora and the oak-madroño forest, it will now be desirable to outline the climatic conditions which they indicate, since an accurate knowledge of the climatic conditions during the Mascall epoch may be expected to throw light on the age of the Mascall formation. The annual rainfall at Jasper Ridge is given by Cooper as about 32 inches, most of it falling during the winter, with a season of prolonged drouth during the summer. The temperature is mild and has a low seasonal range. If it may be assumed from the close relation of the Mascall flora to the broad-sclerophyll forest that the annual rainfall in eastern Washington and Oregon, southwestern Idaho, northwestern Nevada, and northeastern California was about 30 inches during the Mascall epoch, the inference may be drawn that the climate was less moist at this time than during the preceding Bridge Creek epoch, and that it was considerably more humid than it is in these regions at the present time. The climate during the Bridge Creek epoch, in the Upper Oligocene, was sufficiently moist to permit the growth of a typical redwood forest essentially like that now occupying the coastal strip of central and northern California, where the rainfall averages about 40 inches annually, although it is considerably less toward the south of the Redwood Belt and more toward the north. A reduction of about 10 inches of rainfall is therefore suggested by the Mascall flora. Since the Mascall epoch, the rainfall has been further reduced in the Great Basin Province, now averaging about 15 inches. The evidence of the plants as furnished by the Bridge Creek, Mascall, and modern floras for the time from the Upper Oligocene to the present, indicates a trend toward aridity, probably though not of necessity continuous. This indication is in general agreement with the evidence as to progressive aridity during the Tertiary suggested by the character of the sedimentary deposits and by the development of the mammals. In view of the border relationship already indicated between the modern oak-madroño and redwood forests, it would be anticipated that a reduction of 10 inches of rainfall during the Tertiary would have resulted in a change from a redwood type of forest to an oak-madroño forest, which is precisely what the plant record shows. What may actually be supposed to have happened was a gradual depletion in numbers of the redwoods which dominated the forest during the Bridge Creek epoch and an advance toward the stream borders of the oaks, madroños, and their associates, until they were in a position during the Mascall epoch to place their leaves in the sedimentary record. A present-day example of such a change in forest composition has already been noted at Jasper Ridge, where oaks, madroños, maples and their associates are now dominating the stream course along which there remain

scattered *Sequoia* relicts, and where both the conifers and the broad-leafed types are entering the stream deposits.

If it is supposed that there was a further reduction in rainfall following the Mascall epoch, and the evidence of the sediments and the vertebrate fauna of the overlying Rattlesnake formation appears to be consistent with this view, it may be assumed that there was a further change in the character of the vegetation. Since at the present time the oak-madroño forest grades into the chaparral to the south, where the rainfall is considerably less, it is fair to assume that the climax formation of the Rattlesnake epoch may have been of the chaparral type. Unfortunately there is no known record of the flora of the Rattlesnake formation; its very absence from the sediments in a considerable number of localities which have been examined suggests the type of arid climate which would have supported a chaparral flora and, at the same time, because of the dryness, have made difficult the preservation of fossil leaves in the record. For in a semi-arid region the intermittent character of the water bodies is a disadvantage in the process of leaf-fossilization, since with their exposure to the atmosphere the leaves tend to decay before their impressions have been left in the sediments. While the negative evidence of the Rattlesnake is in accord with the general idea of a continued trend toward aridity following the Mascall epoch, it is not so suggestive as the evidence of the actual presence of Pliocene floras in California.

In the Sonoma tuffs near Santa Rosa, commonly considered to be of Lower or Middle Pliocene age, the writer has made small collections of leaves which are here named rather definitely as to genera. In the following list the resemblance of these to living species is suggested but without indicating any established identity:

| | |
|---|---|
| Castanopsis (cf. chrysophylla) | Quercus (cf. densiflora) |
| Cornus (cf. pubescens) | Sequoia (cf. sempervirens) |
| Platanus (cf. racemosa) | Woodwardia (cf. chamissoi) |
| Populus (cf. trichocarpa and fremontii) | |

While this list is made up for the most part of genera which characterize the Mascall assemblage, the relative scarcity of *Sequoia* and the dominance of *Platanus* of the *racemosa* type indicates a much less humid habitat. Whereas the Mascall species, *P. dissecta,* is related so far as leaf characters are concerned to the living *P. occidentalis,* which is a typical mesophyte, the Sonoma tuff species has its affinity, as above suggested, with *P. racemosa,* which occupies semi-arid regions and without regard to the ranges of the living related species, the small size and essentially entire margin of the Sonoma tuff *Platanus* suggests a less humid habitat than does the larger serrate-margined *P. dissecta* of the Mascall assemblage.

As mentioned above, a fossil flora has been described by Hannibal from the Santa Clara formation, in the Coast Ranges south of San Francisco Bay, about 75 miles south of Santa Rosa. On the basis of its stratigraphic relations and of its molluscan fauna, the Santa Clara formation has been referred to the Upper Pliocene, although it may possibly be referable to the Pleistocene. In any case it appears to be younger than the Sonoma tuff on the basis of its stratigraphic relations. The flora as described by Hannibal has a distinctly xerophytic aspect, and includes several species of the chaparral and chaparral border. Through the courtesy of Professor J. P. Smith, the writer has recently been able to study Hannibal's collections at Stanford University. The following is in no sense to be considered as a final revision, but constitutes, in the opinion of the writer, a more accurate list of the plants represented than that in Hannibal's paper:

| | |
|---|---|
| Pseudotsuga? (cf. taxifolia) | Quercus (cf. chrysolepis) |
| Sequoia (cf. sempervirens) | Ribes (cf. menziesii) |
| Salix (cf. lævigata) | Cercocarpus (cf. parvifolius) |
| Salix (cf. fluviatilis) | Amelanchier (cf. alnifolia) |
| Populus (cf. trichocarpa) | Ceanothus (cf. integerrimus) |
| Alnus (cf. rhombifolia) | Arbutus (cf. menziesii) |
| Quercus (cf. agrifolia) | Symphoricarpus (cf. racemosus) |

From the occurrence with the plant fossils of lacustrine types of mollusks, this assemblage may be considered to have occupied the shores of small lakes. The absence of broad-leaved oaks and the scarcity of the remains of redwoods indicate a more xerophytic assemblage than of the Mascall. The relative abundance of the evergreen oaks and the presence in the record of such chaparral forms as *Cercocarpus and Ceanothus,* indicate decidedly xerophytic conditions, such as those on the south slopes in this region to-day. Altogether, the Santa Clara flora as now known is indicative of a more arid climate than that of any of the fossil floras previously considered.

Of still greater significance, because of its close proximity to the region where the Mascall flora is typically present, is the small flora collected by Miss Alexander and Miss Kellogg near Alturas. The late Pliocene age of this flora appears to be indicated by the associated mammalian remains; the close similarity between the two fossil plant species of poplar and willow and species of these genera now living in the northern Great Basin is wholly consistent with this age reference. *Populus trichocarpa* and *Salix fluviatilis* are at the present time the most common trees along the John Day River and other streams in this general region, and their leaves appear more likely to enter the sedimentary record than those of any other species. So far as the evidence of this small flora goes, it indicates conditions not unlike those now obtaining in the John Day Basin, with a rainfall of hardly more than 15 inches annually.

The climatic suggestions of the floras from the Upper Oligocene to the present may be summarized as follows:

| Plant assemblages. | Rainfall indicated. |
|---|---|
| Present flora of the John Bay Basin | 15 inches. |
| Alturas flora, Upper Pliocene | 15 inches or more. |
| Santa Clara flora, Upper Pliocene | 20 inches or less. |
| Sonoma tuff flora, Lower or Middle Pliocene | 20 inches or more. |
| Mascall flora of the John Day Basin | 30 inches. |
| Bridge Creek flora, Upper Oligocene of the John Day Basin | 40 inches. |

If the conclusions regarding the rainfall indications of these fossil floras, as based on the moisture requirements of their living equivalents, are correct, and if the floras are at all typical for the Tertiary of the western United States, two suggestions may be made—first, that there was a progressive trend toward aridity in the Great Basin and perhaps to some extent in west-central California, during the Tertiary; and second, that the age of the Mascall flora is Miocene, as indicated by its intermediate position in the scale of rainfall. The presence in the Mascall flora of genera no longer living in the western United States also suggests that it is as old as Miocene.

Fortunately there is ample corroboration of these suggestions of the Miocene age of the Mascall flora in the evidence of the stratigraphy and the associated fossil mammals. The stratigraphic evidence of the Miocene age of the Mascall flora may be briefly summarized as follows: The flora occurs in shales overlying the Columbia lavas, commonly considered to be of Miocene age, at Rock Creek near the type locality of the Mascall formation in the John Day Basin, in the Blue Mountains at Austin and Tipton, in the Payette localities in Idaho, and at Ellensburg, Washington. At the first two localities named, the Mascall beds underlie the Rattlesnake rhyolite, which has been referred to the Pliocene; the Payette formation is overlaid by a rhyolite upon which rest sedimentary beds containing a Pliocene fauna; there is no rhyolite associated with the Ellensburg formation. At the Spokane locality the leaf-bearing beds are considered to be contemporaneous with the Columbia lavas, although the lava series lying to the west may represent something more than the Columbia lavas as recognized in the John Day Basin and elsewhere. The other localities are not associated with rocks which can be determined as either Columbia lavas or Rattlesnake rhyolite; basalt flows overlie the leaf-bearing shales both at Forty-nine Camp, Nevada, and Trout Creek, Oregon.

The type locality of the Mascall fauna, commonly considered to be of Middle Miocene age, is less than a mile from the Rock Creek locality of the Mascall flora, where the indications are that the plant-

bearing layer underlies the rest of the Mascall formation. An Upper Miocene fauna has been found in the Ellensburg formation several hundred feet above the plant-bearing layers. Vertebrate remains collected from the Payette formation are considered to be of Middle or Upper Miocene age. Associated vertebrates at Trout Creek have been referred to the Oligocene or Miocene. The *Hipparion* remains from the locality at Tuolumne Table Mountain appeared to indicate the Pliocene age of the gravels, over which occur the tuffaceous sediments containing the plants. But there is increasing evidence, as recently presented by Matthew,[1] of the presence of *Hipparion* in the Miocene which makes a Pliocene reference decidedly uncertain in this case. No associated vertebrates have been found at the Blue Mountains, Spokane, and California Coast Range localities, although there is an invertebrate fauna associated with the plants at the last-named locality which is considered to be of Miocene age. In the main, the evidence of associated faunas indicates the Middle Miocene age of the Mascall flora, although certain elements of it, notably that at Tuolumne Table Mountain and possibly those at Forty-nine Camp and Pitt River, may be as young as early Pliocene.

## SUMMARY AND CONCLUSIONS.

The Mascall flora is distributed over an area in the West 700 miles north and south and 250 miles east and west. It is most common in the Great Basin portions of Washington, Oregon, Idaho, Nevada, and California, but occurs also in west-central California, where its composition is less typical than in the Great Basin. There is a total of 45 species represented, of which 11 are by far the most abundant and widespread. Since the record of the distribution of these species in rocks of known age elsewhere does not give conclusive evidence of the age of the Mascall flora, the climatic significance of the assemblage as a whole is considered with relation to the climatic data for known portions of the Tertiary. A comparison of the Mascall assemblage with the modern oak-madroño forest of the West indicates so close a resemblance that the rainfall of the Mascall epoch may be considered to be essentially the same as that in this forest at the present time, about 30 inches annually. This amount is less than the rainfall indicated by the Upper Oligocene Bridge Creek flora, more than that indicated by the Pliocene floras of California, and much more than that now recorded from the Great Basin; there is seen to be a regressive successional change in the floras through the Tertiary and up to the present time which is quite in accord with the evidence of progressive aridity based on studies of the sedi-

[1] W. D. Matthew, Correlation of the Tertiary Formations of the Great Plains, Bull. G. S. A., vol. 35 pp. 752–753, 1924.

mentary record and the mammalian remains. Its climatic position in this series of floras strongly suggests the Miocene age of the Mascall flora. This reference is supported by the relatively primitive character of the Mascall sycamore, *Platanus dissecta*, as compared with the Pliocene species, which is closely related to the living *P. racemosa*. The record of the presence in the Mascall flora of a considerable number of genera which are no longer found in the western United States is also in accord with this age reference. The evidence of the stratigraphic position of the Mascall formation and the vertebrate fauna occurring in it is, on the whole, consistent with the reference of the Mascall flora to the Middle or Upper Miocene.

In view of the fact that the principal dicotyledonous leaf-types appear to have been well established by the early Tertiary in the West, it may be too much to expect that any definite phylogenetic trend can be recognized in leaves which will have as great stratigraphic value as this trend in such mammalian families as the Equidæ. Since trees appear to have remained fairly stable during the Tertiary, the changes in floras from one to another Tertiary period may probably be best interpreted as representing changes in distribution due to environmental causes, of which rainfall was the most important. As there is wholly independent evidence of a trend toward aridity from the Oligocene to the present in the Great Basin, based on the changes in character of the sediments and the mammalian faunas, this environmental factor appears to be wholly adequate to provide for many of the changes recorded in the plant assemblages during this time. This being the case, an ecological interpretation based on a fossil flora whose taxonomic content has been critically determined may have great value in establishing its stratigraphic position in the Tertiary. It may ordinarily be assumed that a fossil flora represents the climax forest formation, since this type of forest will be most favorably situated to leave a record of its presence in the sediments, because of its proximity to lakes and rivers. Since a widespread climax forest is an indication of low relief and uniform climate at the present day, the wide distribution of the Mascall flora has a significant bearing on the topographic and climatic conditions in the western United States during the Miocene.

FIG. 1.—Type locality of Mascall flora in John Day Basin, Oregon.

FIG. 2.—Oaks, madreño, and associated conifers in subclimax forest of northern California.

III.

# NOTES ON TWO FOSSIL HACKBERRIES FROM THE TERTIARY OF THE WESTERN UNITED STATES.

By RALPH W. CHANEY.

With one plate.

# NOTES ON TWO FOSSIL HACKBERRIES FROM THE TERTIARY OF THE WESTERN UNITED STATES.

By Ralph W. Chaney.

## I. A NEW FOSSIL LEAF SPECIES FROM THE JOHN DAY SERIES OF OREGON.

The recent discovery of a Tertiary species of *Celtis* in Oregon is of interest in view of the small number of fossil representatives of this genus described in North America. Only five species have been previously recorded, *Celtis lingualis* and *C. newberryi* from the early Eocene Fort Union formation of Wyoming; *C. mechoshii* from the Florissant beds of Miocene age in Colorado; *C. pseudo-crassifolia* from the Pleistocene of Maryland; and *O. mississippiensis* from the Pleistocene of Mississippi. The wide geologic range of these fossil species, from the base of the Tertiary up to the present, together with the extensive geographic distribution of both the fossil and the living forms, indicates that hackberries have probably been present in North America continuously since the beginning of the Tertiary, and that they may have been much more wide-spread than the fossil record would indicate.

The Bridge Creek flora, which has its best development in the John Day Basin of eastern Oregon, is noteworthy both because of its close resemblance to the redwood forest now occupying the Pacific Coast from central California to southern Oregon, and because of its wide distribution in North America, Eurasia, and the Arctics. Its association with beds bearing a well-known vertebrate fauna in the John Day region indicates that the age of this flora is Upper Oligocene. Associated with the redwoods, alders, tan-oaks, and bays, which make up a dominant part of the Bridge Creek assemblage, there are a number of forms that have no living representatives in the redwood forest of to-day. Among these is a species of hackberry, here described as new, to which the name *Celtis obliquifolia* is given.

The relative scarcity of its leaves in the fossil record suggests that this species was not abundant in the Bridge Creek forest. At the type locality on Bridge Creek there were only 6 specimens in the total of 20,611 counted.[1] At the Gray's Ranch locality on the

[1] R. W. Chaney, Quantitative studies of the Bridge Creek flora, Am. Jour. Sci. VIII, p. 131, table II, Aug., 1924.

Crooked River not far to the south, where deposits of similar age have been found, the number of leaves of the hackberry is considerably greater, although no exact figures can be given. There is increasing evidence that most fossil leaves of all species, at least in the Tertiary of the West, come from trees which grew in the immediate vicinity of rivers, lakes, or other sites of deposition. It may therefore be supposed that *Celtis obliquifolia* either was a rare associate of the redwood, alder, and other typical forms along the stream or lake borders of the Bridge Creek forest, or that it lived for the most part on the slopes away from the sites of deposition. Evidence will later be introduced to indicate that the second alternative is the more likely.

Plate I supplements the following description of *Celtis obliquifolia*, and emphasizes its resemblance to *C. reticulata* and *C. douglasii*, two living species whose leaves are also figured.[1]

**Celtis obliquifolia**, new species.

Leaves broad ovate to oblong-ovate, acuminate, distinctly asymmetrical at the base which is slightly sub-cordate and has an obliquely truncate appearance; length from 5 to 13.5 cm., width from 2.2 to 8 cm., average dimensions about 9 by 3.5 cm.; margin commonly entire, in some leaves with broad crenulations, serrate in a few individuals; petiole averaging slightly over 1 cm. in length, and probably stout as indicated by its frequent occurrence attached to the blade; midrib medium stout, commonly straight, in some cases slightly bent at the point of attachment of the upper secondaries, and curving at the apex; 8 to 10 pairs of secondaries, the lower pair leaving the midrib at its base, the upper pairs sub-opposite, leaving the midrib at an angle of 35° and curving near the margin to form conspicuous loops with the secondaries next above; tertiaries in the main percurrent, strongly developed on the basal sides of the lower pair of secondaries, with loops at the margin; the lowest two or three of these basal tertiaries commonly branching off at or near the point of attachment of the lower pair of secondaries with the midrib, giving a suggestion of palmate nervation; leaves probably thin, as indicated by the distinctness of the nervation, although the undulate margins of certain specimens carry a suggestion of semi-coriaceous texture.

*Localities:* Bridge Creek, 9 miles northwest of Mitchell, Oregon, and Gray's Ranch on the Crooked River, 11 miles east of Post, Oregon, in shales referred to the lower division of the John Day series.

There are 75 species of the genus *Celtis* now living and widely distributed throughout the northern hemisphere. Of the 6 species living in the United States, only *C. pumila* fails to reach the western or southwestern states. While certain of these species, more notably *C. occidentalis* and its varieties, grow in moist places, the forms now living in the western United States show an ability to exist under climatic extremes too rigid for most deciduous species and are characteristically found along streams in semi-arid and arid regions. This is true both of *C. reticulata* and *C. douglasii*, to which species the fossil

[1] *C. douglasii* is considered only a variety of *C. reticulata* by some botanists.

appears to be most closely related. The distribution of *C. douglasii* is described as follows by Sargent[1]:

> Dry hillsides and rocky river banks; eastern Oregon from the valley of the Des Chutes and Columbia Rivers to the cañon of the Snake River, Whitman County, Washington, and to Big Willow Creek, Canon County, western Idaho; on the western foothills of the Wasatch Mountains, in the cañon of Grand River, and in Diamond Valley, Utah; southern California, near Independence, Inyo County, Hackberry Cañon, Kern County, and Things Valley at base of Laguna Mountain near Campo, southern San Diego County; on Cedros Island, and in northern Lower California; rim of the Grand Cañon, Arizona; and on the eastern foothills of the Rocky Mountains of Colorado. Occasionally planted in the towns of western Washington, and when cultivated said to grow into a larger and more shapely tree with thinner leaves.

*C. reticulata* has a similar habitat in Texas, Oklahoma, New Mexico, and Arizona. *Celtis douglasii* occurs as a small tree with small thick leaves along the John Day River within a few miles of the Bridge Creek fossil locality. The larger size and thinner texture of the leaves of the fossil *C. obliquifolia* suggests a more favorable habitat, comparable to that mentioned by Sargent in western Washington. This type of habitat is amply indicated also by the other fossil forms of the Bridge Creek assemblage, which as above stated make up a community closely similar to the redwood forest now occupying coastal California, where the rainfall varies from 20 to 60 inches annually. In the course of the gradual desiccation of this northern portion of the Great Basin since the Oligocene, most of the characteristic redwood associates have disappeared from eastern Oregon. These include the redwood (*Sequoia langsdorfii*), the tan-oak (*Quercus consimilis*), the bay (*Umbellularia oregonensis*), and other forms whose modern equivalents are now living only near the Pacific Coast or in the Sierra Nevada, as well as the elm (*Ulmus speciosa*), the basswood (*Tilia* sp.), and the hornbeam (*Carpinus grandis*), whose modern equivalents are now restricted to the eastern United States. In the group of hardier forms which, like *Celtis obliquifolia*, were able to remain in the region by adjusting themselves to a more arid environment, may be mentioned *Crataegus flavescens*, *Philadelphus* sp., and *Rosa hilliae*, all of which have generic representatives growing along the streams in the John Day Basin to-day, and *Pinus knowltoni*, *Corylus macquarrii*, *Alnus carpinoides*, *Acer osmonti*, and *Cornus* sp., whose modern equivalents are now living in the nearby Blue Mountains.

The relative scarcity of the leaves of *Celtis obliquifolia* in the Bridge Creek shales suggests that even during the Oligocene this species had its most characteristic situation on the borders of the forest, well away from the sites of deposition and that it can hardly be considered to have been a typical member of the mesophytic redwood consociation.

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[1] Manual of the trees of North America, p. 322.

## II. DESCRIPTION OF A FRUIT SPECIES FROM THE WHITE RIVER FORMATION OF SOUTH DAKOTA.

There is a conspicuous lack of fossil plants in the Oligocene and Miocene rocks of the northern Great Plains, a situation which has been difficult to explain in view of the abundance of the plant record in rocks of this age farther to the west. Except for silicified wood, the only fossil plants known to the writer from the Oligocene and Miocene of South Dakota and Nebraska are hackberry fruits which occur in great numbers as casts filled with calcite. These are here described for the first time, both to put them definitely on record and to bring out certain theoretical considerations relating to the climate under which they lived and the possible cause of the absence of other plant fossils.

The first mention of hackberry fruits in the Tertiary of the Great Plains appears to have been made by Hatcher in 1902.[1] In a recent paper on the White River beds of South Dakota,[2] Wanless has referred to them in his discussion of the physiography and climate of the White River epoch. Several years ago W. J. Sinclair sent to the writer a number of these fruits which he collected in the White River beds of South Dakota. Their description follows:

**Celtis hatcheri,** new species.

Nutlets spheroidal to ovate-spheroidal, slightly flattened, the outer portion, representing the fleshy layer, shrunken and covered with conspicuous reticulate ridges of which the more conspicuous are longitudinal, with smaller ridges, which divide the surface into numerous small polygons; produced into a short point at the distal end, and with an inconspicuous attachment scar at the basal end; diameter 3 to 5 mm.; thickness of the shrunken fleshy layer about 0.4 mm.; interior more or less completely filled with calcite crystals, and with no seed structure showing in the specimens examined.

*Locality:* Big Badlands, South Dakota, from the Lower Oreodon beds of the White River formation.

These fruits are on the average slightly smaller than those of *Celtis douglasii* and their surface markings resemble those of this and several other living species as shown by figures 7 and 8, plate I.

Wanless mentions the occurrence of hackberry fruits in millions in the clays of Oreodon beds. They have also been found by the writer in great numbers in the Sheep Creek beds of Miocene age, near the Agate Springs quarry in Nebraska, and are reported by Cook[3] at various horizons in Nebraska, including the Pleistocene. Their presence is significant in view of the scarcity of other plant remains of similar age in this region, suggesting climatic and depositional conditions not unlike those in the drier parts of the West at the present time. A variety of the common hackberry, *Celtis occi-*

[1] Proc. Amer. Phil. Soc., vol. 41, pp. 113-131, 1902.
[2] Proc. Amer. Phil. Soc., vol. 62, pp. 236-237, 1923.
[3] Personal communication of January 14, 1925.

*dentalis* var. *crassifolia*, is found to-day along the streams in western South Dakota and, as above mentioned in the discussion of *Celtis obliquifolia*, most of the American hackberries range into the semi-arid portions of the West, where they are characteristic stream-border trees of small size. Among the more common associates of the hackberries in these regions are several species of *Populus* and *Salix*. There is little likelihood under present climatic conditions of any of the leaves of these trees becoming a part of the fossil record, since in most cases they become dried and decayed before they have left their prints in the sediments accumulating along the streams. The fruits of most of these stream-border species are small and thin-shelled or fleshy, and are ill suited to enter permanently into the sedimentary record. The only exceptions known to the writer are the hackberry and the cherry, both of which have hard-shelled seeds which might be expected to remain in the sediments long enough to leave a mold or even to be replaced by calcium or silica. There is, however, no known record of the seeds of *Prunus* in the Tertiary of the Great Plains. The presence of a large number of hackberry fruits indicates beyond question the abundance of hackberry trees along the sites of deposition during the Oligocene and Miocene in the Great Plains. At the same time, the absence of hackberry leaves, and of the leaves and fruits of other species which may be supposed to have lived in the same situation, is a strong suggestion of a climate so arid as to prevent their entrance into the sedimentary record.

Stumps and fragments of wood are not infrequently found in the White River beds. Sections have recently been made by the United States Geological Survey of the wood from a stump in the Lower Titanotherium beds at Corral Draw, South Dakota, sent to the writer by Sinclair. It resembles the wood of the living *Celtis occidentalis* in a general way, although it is certainly different specifically, and its final determination as *Celtis* is as yet not fully established. In so far as this tentative determination is correct, it serves to corroborate the evidence of the fruits in showing that hackberries occupied the valleys during the White River epoch.

In the Bridge Creek shales, from which were secured the leaves described as *Celtis obliquifolia* in the first part of this paper, no hackberry fruits have been found. The following explanation may be offered for the difference in character of the *Celtis* record in the Bridge Creek shales and in the White River clays. The Bridge Creek shales were laid down in a moist region, as indicated by the character of the flora as a whole, and the hackberry trees appear to have occupied the forest borders and the slopes at some distance from the water bodies. From here a few leaves might be transported by the wind and lodged in the streams or lakes, but the chances for the transportation of small spherical fruits for an equal distance was

slight. As a result the Bridge Creek record comprises leaves only. The White River clays were laid down in an arid or semi-arid region, as indicated by the almost complete absence of fossil leaves, and the hackberry trees occupied the immediate borders of the intermittent water bodies. They were in a position here to lodge both leaves and fruits in the stream or lake deposits, but the leaves were dried and decayed leaving only the record of the fruits in the sediments.

The suggestion may be made on the basis of the fossil and living hackberries that climatic changes and the resultant vegetational development in South Dakota and Oregon have been somewhat similar from the Tertiary up to the present time, but that in Oregon they have lagged behind the changes in South Dakota. In the Great Plains there is an Eocene record of the presence of two leaf species of *Celtis* in the Fort Union formation. From the size and the marginal characters of these leaves, the climate may be supposed to have been moist, an indication amply borne out by the mesophytic assemblage of plant remains which occur with them as fossils. By Oligocene and Miocene times the rainfall had been cut down to a point where no leaves could enter the fossil record, so far as is known, and where the only remains of fossil plants are abundant hackberry fruits and occasional stems. This semi-arid climate appears to have continued down to the present in the Great Plain. In the John Day Basin during the Oligocene, a high rainfall is indicated by the fossil plants making up the redwood association, and conditions were suitable for the entrance of hackberry leaves into the sedimentary record. There are evidences of progressive aridity throughout the northern portion of the Great Basin following the Oligocene,[1] until at the present time this rainfall has been reduced to less than 15 inches, with the result that most of the trees of the Tertiary have either disappeared completely from the region or are found only in the nearby mountains. Of those species which remain, *Celtis douglasii* appears to have the best chance of leaving a record in the contemporary sediments, since it grows near the streams and has a hard-shelled fruit which may persist even though leaves and less substantial fruits become dried and decayed. For some reason, possibly related to a difference in date of the growth of mountain ranges on the side from which the rain came, the drying up of the Great Plains region took place in the Oligocene, at a time when moist forests still covered the surface of eastern Oregon. These forests in turn have disappeared in consequence of a reduction in the rainfall until to-day only a scattered group of hardy trees remains along the stream courses.

[1] See R. W. Chaney, The Mascall flora, its distribution and climatic relation. Carnegie Inst. Wash. Pub. No. 349, pp. 25–48.

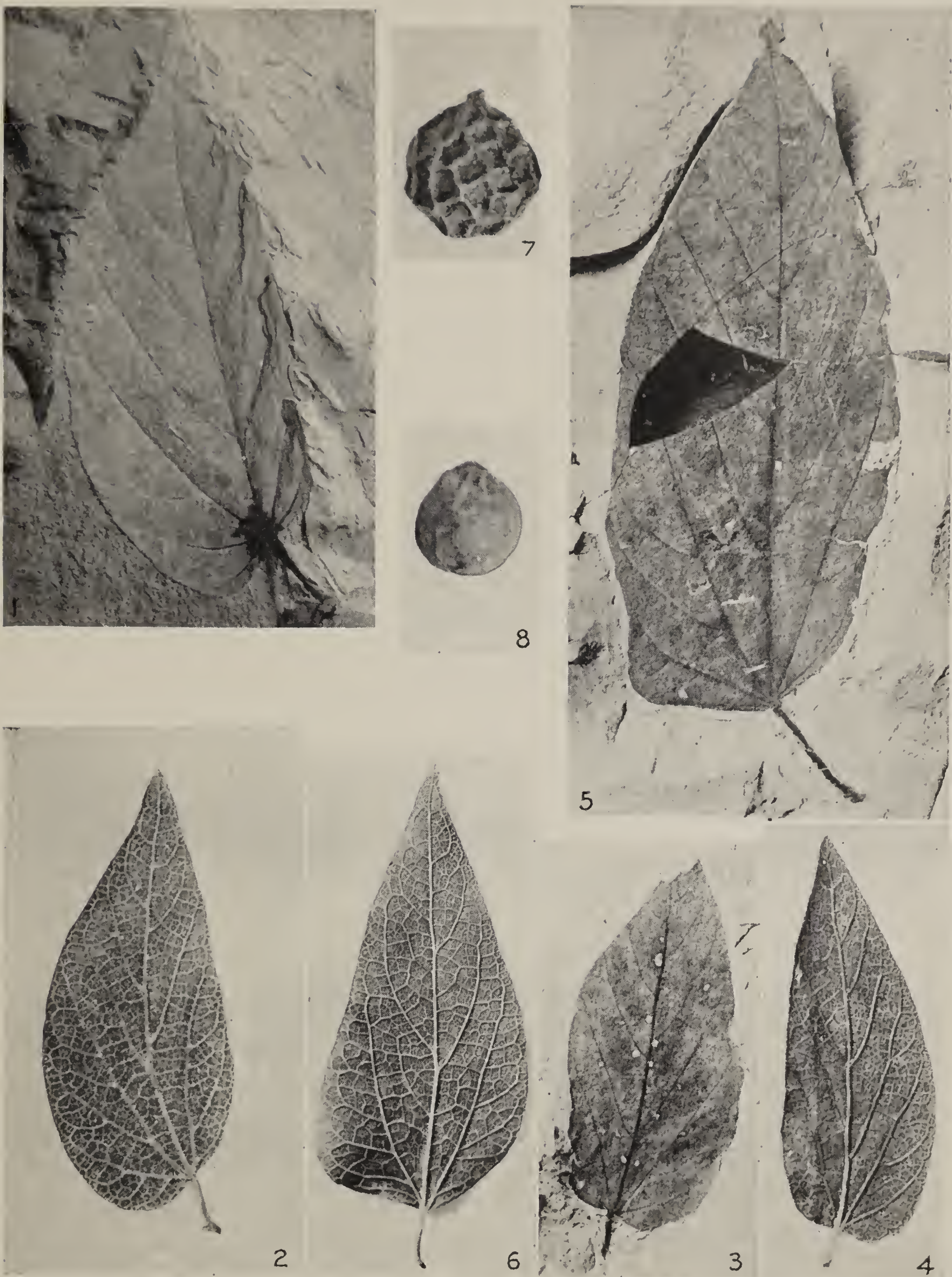

FIG. 1. *Celtis obliquifolia*, n. sp. Specimen of average size and shape from Bridge Creek shale, Gray's Ranch, Oregon.

FIG. 2. *Celtis reticulata* Torr. Living species, from Atascosa County, Texas. From herbarium of California Academy of Sciences, No. 10774.

FIG. 3. *Celtis obliquifolia*, n. sp. Small specimen from Bridge Creek shale, Gray's Ranch.

FIG. 4. *Celtis douglasii* Plan. Living species, from Peach Springs, Arizona. From herbarium of University of California, No. 5861.

FIG. 5. *Celtis obliquifolia*, n. sp. Specimen with broadly cuneate base from Bridge Creek shale, Gray's Ranch.

FIG. 6. *Celtis reticulata* Torr. Living species from Mitchell County, Texas. From herbarium of California Academy of Sciences, No. 13786.

FIG. 7. *Celtis reticulata* Torr. Nutlet of living species. 3×.

FIG. 8. *Celtis hatcheri*, n. sp. Nutlet from White River beds, Big Badlands, S. D. 3×.

IV.

# A RECORD OF THE PRESENCE OF UMBELLULARIA IN THE TERTIARY OF THE WESTERN UNITED STATES.

By RALPH W. CHANEY.

With one plate.

# A RECORD OF THE PRESENCE OF UMBELLULARIA IN THE TERTIARY OF THE WESTERN UNITED STATES.

By Ralph W. Chaney.

The laurel family, comprising 40 genera and 1,000 species, is primarily tropical and subtropical, the chief centers of its distribution being in southeastern Asia and Brazil. Of the five arborescent genera occurring in North America, *Ocotea* and *Misanteca* do not range north of southern Florida; *Persea* reaches Delaware although it is more characteristic of the states farther south; and *Sassafras* and *Umbellularia* are typically temperate in distribution. *Sassafras* ranges from southern Maine and Ontario south to Florida and Oklahoma, having perhaps its best development in the southern states. *Umbellularia* is limited to western California and southwestern Oregon, reaching its greatest abundance and largest size in the latter state.

Only three of these genera have been reported as fossil in North America: a single species of *Ocotea* from the Cretaceous of New York; 14 species of *Persea* ranging from the Cretaceous to the Pleistocene in age, and occurring in Massachsuetts, New York, the southern states, Kansas, Colorado, Wyoming, California, and British Columbia; and 19 species of *Sassafras*, occurring for the most part in the Cretaceous of the Atlantic states and Kansas. Other genera of the Lauraceae have been reported as fossils, which are no longer living in North America, of which *Cinnamomum*, with 30 wide-ranging fossil species, and *Laurus*, with 40, are the most notable. It seems likely that many of these species, and perhaps certain of the generic references as well, are open to question. The failure to recognize the genus *Umbellularia* in the Tertiary of the West has no doubt been due in large part to the fact that most of the earlier workers in palaeobotany were not familiar with the living tree, *Umbellularia californica*, and also to the general similarity of its leaves to several other common genera.

In connection with his studies of the John Day and other Tertiary floras in the West, the writer has collected a considerable number of leaf specimens that appear to be referable to *Umbellularia*. In addition to the close similarity of these leaves to the modern species, the groups of fossil species with which they occur are much like the

communities in which the modern California laurel, *Umbellularia californica*, is living. Thus, the redwood association of the Bridge Creek Oligocene, with its abundant redwoods, alders, and tan-oaks, and the Mascall flora of Miocene age, with its oaks, madrones, and buckeyes, might both be expected to include *Umbellularia* in their assemblages if the distribution of the living species is any criterion.

The presence of leaves of this type in the Bridge Creek flora was first noted by Newberry in 1882[1], under the name *Fraxinus integrifolia.*[2] In his later more complete discussion[3] Newberry expresses some doubt as to whether this is a proper generic reference, a doubt shared by Knowlton[4] in the consideration of *Fraxinus integrifolia* in his bulletin on the John Day floras, where he makes the following statement.

> This species is represented in all the collections from Bridge Creek by a large number of examples which agree exactly with Newberry's types. When the lower surface of the leaves is exposed the nervation shows clearly, but when the upper surface is the one exposed it is impossible to detect a trace of the nervation. This shows conclusively that the leaves were very thick and coriaceous. The upper surface is also minutely wrinkled, as would be the case with a thick, leathery leaf. From these considerations I am inclined to doubt the correctness of referring them to *Fraxinus*, but for the present they may be so retained.

Not only is the texture too thick for a typical member of the genus *Fraxinus*, as pointed out by Knowlton, but the leaves are in all cases petiolate, while the leaflets of *Fraxinus* are commonly sessile on the rachis. Further, the leaflets of *Fraxinus* tend to be less symmetrical than the fossil leaves in question. Inasmuch as these are generically indistinguishable from the living California laurel, *Umbellularia californica*, a new combination is made as follows:

**Umbellularia oregonensis,** new combination.

Leaves elongate-ovate to lanceolate, broadly ovate in the case of the smaller specimens, acuminate to a narrowly rounded emarginate apex, and with a slightly asymmetrical, cuneate base; length from 3.7 to 8.5 cm., width from 1.2 to 2.5 cm.; margin entire, probably slightly thickened as indicated by its undulate character; petiole 2 to 4 mm. long, and commonly present; midrib straight, very stout at the base and becoming distinctly more slender toward the apex; secondaries in 8 or more pairs, sub-opposite, curving well inside the margin and joined above in distinct loops, also several smaller nerves branching off from the midrib between the main secondaries for a short distance and joining with the tertiaries, which form an indistinct network; in some specimens a pair of secondaries branches off near the base and swings parallel with the margin nearly halfway up the leaf; texture probably coriaceous, as indicated by the indistinct character of the nervation in most of the specimens, and by the undulate margins.

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[1] Proc. U. S. Nat. Mus., vol. 5, p. 509, 1882.

[2] The specific name has recently been changed to *oregonensis* by Knowlton and Cockerell because *integrifolia* is a homonym in the case of Newberry's species.

[3] Mon. 35, U. S. Geol. Survey, p. 128, 1898.

[4] Bull. 204, U. S. Geol. Survey, p. 84, 1902.

*Localities:* Bridge Creek, 9 miles northwest of Mitchell, Oregon, and Gray's Ranch on the Crooked River, 11 miles east of Post, Oregon, in shales referred to the lower division of the John Day Series.

The fossil species is closely similar to the living *Umbellularia californica* in general shape, size, and nervation characters, even to having in some specimens the basal pair of secondaries paralleling the margin as above noted. It differs mainly in always having an emarginate tip which is not regularly present in the living species, and in the invariably cuneate character of the leaf base, which is commonly rounded to a slight extent in the living species.

The leaves of the living *Umbellularia* in many ways resemble those of the western chinquapin, *Castanopsis chrysophylla*, which occurs to-day in a similar forest community in western California. They differ in the following respects: (1) the leaves of *Umbellularia* have their greatest width in the lower one-third, while those of *Castanopsis* tend toward obovateness, or at least commonly continue at a maximum width into the upper third of the leaf; (2) the tips of the leaves of *Umbellularia* are narrowly rounded, in some cases emarginate, while those of *Castanopsis* are almost invariably pointed, and never emarginate except in damaged leaves; and (3) the nervation on both surfaces of the leaves of *Umbellularia* is indistinct, while that on the lower side of *Castanopsis*, particularly the primary and secondaries, stands out. Since the fossil leaves are distinctly ovate, with rounded, emarginate tips, and indistinct nervation on both surfaces, there is little question as to their reference to *Umbellularia* rather than to *Castanopsis*.

The lack of any record of the fruits of *Umbellularia* in the Bridge Creek shales is difficult to explain in view of the abundance of fruits in the present-day deposits where leaves are also being accumulated[1]. Doubtless the fleshy pericarp was readily decomposed after burial in the sediments, but the seeds are too large to have escaped notice in the comparatively large amount of fossiliferous shale which has been studied. Possibly certain specimens considered to be the nuts of *Quercus* may be properly referable to *Umbellularia*.

A species of *Umbellularia* occurs also in the Miocene Mascall beds of Oregon and adjacent states. While certain differences in shape of the leaves have been noted, there is still some doubt as to whether they are distinct from *U. oregonensis*, and a complete discussion of their relations will be deferred until a later time.

The living California laurel is largely a tree of the stream borders, from the Sierras down nearly to sea-level. It is one of the characteristic associates of the redwood along the stream courses, where its

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[1] See R. W. Chaney, Quantitative studies of the Bridge Creek flora, Am. Jour. Sci., VIII, p. 135, table III, Aug. 1924.

leaves have been found to make up 13.27 per cent of the total of over 8,000 leaves counted in basins of deposition[1]. In a count of over 20,000 fossil specimens at the Bridge Creek locality, *Umbellularia integrifolia* made up 8.82 per cent, indicating that its representation in the Oligocene redwood forest was on the same order as that of the living species in the related forest of western California. The very abundance of its leaves in the Bridge Creek shales indicates that *Umbellularia oregonensis* lived on the borders of the water bodies where its leaves could readily enter the sedimentary record.

[1] Op. cit. p. 135, table iii, and p. 131, table ii.

## Description of Plate 1.

Fig. 1. *Umbellularia oregonensis*, n. sp. Specimen of average size and shape from Bridge Creek shale, Gray's Ranch, Oregon.

Fig. 2. *Umbellularia californica* Nutt. Specimen from tree in redwood forest of Del Norte County, California.

Fig. 3. *Umbellularia oregonensis*, n. sp. Elongate specimen from Bridge Creek shale, Gray's Ranch, Oregon.

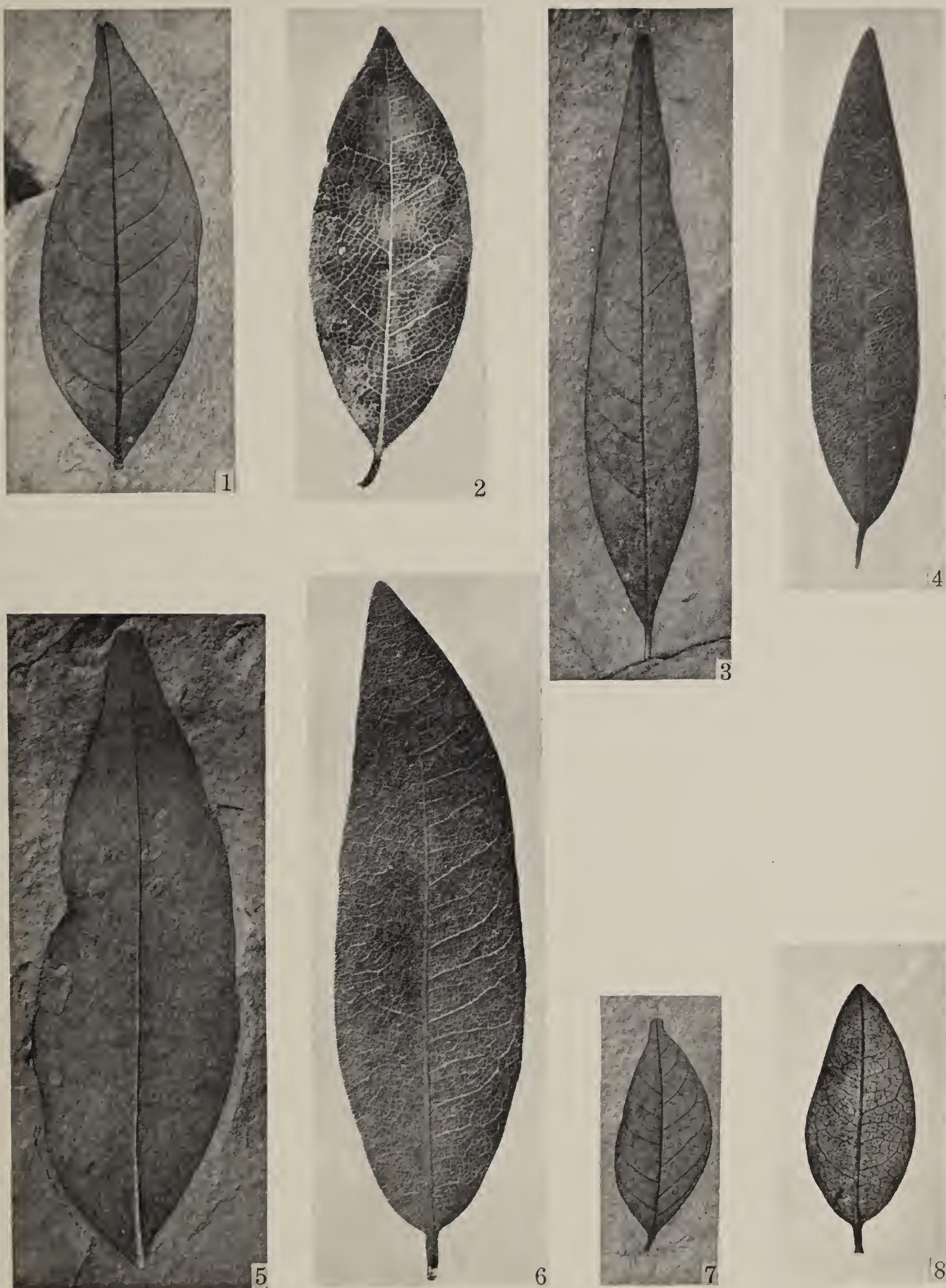
Fig. 4. *Umbellularia californica* Nutt. Elongate specimen from tree on University of California campus, Berkeley, California.

Fig. 5. *Umbellularia oregonensis*, n. sp. Large specimen from Bridge Creek shale, Gray's Ranch, Oregon.

Fig. 6. *Umbellularia californica* Nutt. Large specimen from same tree on University of California campus.

Fig. 7. *Umbellularia oregonensis* n. sp. Small specimen from Bridge Creek shale, Gray's Ranch, Oregon.

Fig. 8. *Umbellularia californica* Nutt. Small specimen from same tree on University of California campus.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# V.

# THE BIRDS OF RANCHO LA BREA.

By LOYE MILLER.

With six plates and twenty text-figures.

# CONTENTS.

# THE BIRDS OF RANCHO LA BREA.

By Loye Miller.

## INTRODUCTION.

A period of seven years has now elapsed since the first description of bird remains from Rancho La Brea. During this time six different institutions have made more or less extensive excavations in the locality and, besides the great mass of mammal remains, have assembled bird remains aggregating at the most conservative estimate more than 100,000 specimens. This material has all been generously placed at the disposal of the writer for study. Comparative material representing Recent species, both native and foreign, has been assembled in much greater amounts than was at first available. Long practice in discriminating between species upon osteological grounds has confirmed certain conclusions while it has condemned others. Therefore, although the Rancho La Brea birds present many problems as yet unsolved, it would seem proper to offer at this time a resurvey of the entire situation as it now stands.

Reports on most of the species from the Asphalt have been published in earlier bulletins. The present effort is put forth to coördinate and to substantiate results previously announced. Several species have been added to the fauna as formerly recorded and apologies are offered for one synonym, *Pleistogyps*, imposed upon the literature of ornithology.

Some material, notably that representing passerine birds, may perhaps never be determined because of the total lack of association of different skeletal segments of the same individual. An unassociated bone of a passerine bird might with equal propriety in many cases be assigned to any one of several species or genera of birds at once distinguishable upon other than osteological grounds. Delay of publication until all questions had been answered would amount to an indefinite postponement of the announcement of some more important conclusions.

## ACKNOWLEDGMENTS.

It is a pleasure to acknowledge indebtedness to the many who have in a variety of ways generously assisted in making lighter a very difficult task. Dr. John C. Merriam, formerly of the University of California, under whose general guidance the work on fossil. birds has been done, has given of his interest and counsel without

restriction. Director F. S. Daggett, late of the Los Angeles County Museum of History, Science, and Art, rendered every possible aid during the work on the immense collection of fossil birds at that institution. The unfailing courtesy of each member of the staff at the American Museum of Natural History, at the United States National Museum, and at the museums of the Universities of Yale and of Princeton, was greatly appreciated.

The efforts of Dr. Joseph Grinnell and Mr. H. S. Swarth, of the California Museum of Vertebrate Zoology, together with valuable assistance from a large number of members of the Cooper Ornithological Club, have added much to the available osteological material used for comparison.

Mr. L. E. Wyman has gone to great pains in photographing material in the Los Angeles collections.

Most of the text-figures are reprinted from earlier papers in University of California Publications, Bulletin Department of Geology.

## GENERAL CONSIDERATIONS.

As a result of the continued study of such great masses of material certain advantages accrue to the worker in clarifying his vision and in maturing his judgment of values, there also develop certain truths which remain hidden under other conditions. Limits of variability can be fairly well determined. The remarkable constance of certain characters becomes evident. Relative abundance of the various species is more or less accurately recorded. What was at first possibly considered a chance occurrence becomes positive as the occurrence is oft repeated.

The student of Recent ornithology, in his effort to unravel the problem of relationships of the greater groups, finds himself confronted by a phylogenetic tree bearing almost parallel branches. In his search for intermediate forms he is not sure that the obliquity of the newly discovered branch shows actual direction of descent or merely the external pressure of homoplasy. He turns properly to palaeontology for aid in his difficulty. Rancho La Brea offers instances which well illustrate these opposite possibilities of the intermediate form.

For example, *Parapavo* appears in the Asphalt as an intermediate between the Old and the New World phasianids. It is maintained that here we have a true intermediate of divergence and not of convergence. Relationship is displayed by a combination of characters which are not visibly adaptive, hence not the reflection of habit or of environment, also it may be noted that the geographic location of the Asphalt beds is in the natural line of biologic diffusion between the Indian habitat of *Pavo* and the Central American habitat of *Agriocharis*. *Parapavo* is, next to the raptors, the most

abundant bird of the Asphalt, while bones referable either to *Parapavo* or to *Meleagris* occur in the Pleistocene of Potter Creek Cave. Phasianids seem thus to have formed an important part of the Pacific Coast avifauna during Pleistocene time.

Of quite a different nature from the preceding case is that of *Teratornis*. This great bird was first known from the skull which displayed a curious mingling of cathartine and aquiline characters, so that its relationships were at first obscure. Certain combinations of characters seemed to ally it with *Serpentarius* and remove it far from the cathartine type. The cranium in cathartines is long, narrow, and high, the beak is broad and depressed. To these characters a sharp contrast is offered by the short, broad cranium and the narrowly compressed beak of the eagles. In *Teratornis* the flattening of the cranium and the compression of beak surpass that seen in any of the North American eagles; thus a decided aquiline aspect was given the head. However, as more of the skeleton and better preserved specimens of the skull became known, the relationship with the cathartids became more evident and *Teratornis* may now be properly considered an aberrant cathartiform with superficial aquiline semblance, a sort of sheep in wolf's clothing.

While the Pleistocene age of the Asphalt beds is too youthful to afford forms ancestral to the larger systematic groups, some interesting light is thrown upon the history of existing species and subspecies. In many instances the living species can be traced back into the Pleistocene, unchanged so far as osteological characters give evidence. What may have been the plumage changes, not even surmise is permissible. In a number of cases, however, the factors of size and proportions, which in ornithology aid in the separation of a species into geographic races, are found to be characters of extreme variability in its Pleistocene phase. Two or more Recent geographic races seem to have sprung from the same highly variable Pleistocene stock. The time of such divergence is thus narrowed down to upper Pleistocene and Recent time. The first case of this sort noted is that of *Haliaëtus leucocephalus*. This eagle is to-day recognized to exist in two geographic races, a Sonoran small race and a Canadian large race, quite distinctly set off from each other in space. In the Asphalt lenses of Rancho La Brea, *Haliaëtus leucocephalus* occurs as a species so highly variable as to embrace a maximum and a minimum extending beyond the limits of the large and the small geographic races of to-day. The same is found to be true of the great horned owl, *Bubo virginianus*. A southern small race, *B. v. pacificus*, and a northern large race, *B. c. saturatus*, are easily included in the highly variable Pleistocene phase of this splendid owl.

The study of a large fauna, such as that of Rancho La Brea, gives one a very positive impression of the great abundance of individuals

as well as of species, a condition comparable to that conceded to Pleistocene mammals. In her Recent fauna California harbors almost 65 per cent more varieties of birds than of mammals. Mammalian remains from the Pleistocene indicate a great abundance—almost an extravagance—of mammals as compared with the present. No less so do we see the avifauna of that time exceedingly rich in those large forms which are more commonly preserved. *Parapavo* was abundant but has left no successor in the region. Cranes, ducks, geese, swans, storks, herons were in abundance, apparently greater than at present. The 7 cathartiform vultures have left but 2 of their number to carry on their function, while no less than 6 eagles, 2 Old World vultures, a caracara, and numerous large hawks have entirely disappeared from the stage. Bird remains are so infrequently recorded that one perforce concedes that this picture of abundant Pleistocene bird life represents but meagerly the truth of the matter regarding its variety and abundance.

The greatest contributions that have been made of late to avian palaeontology have been those bearing on geographic distribution—a most complex set of problems. The bald statement that at least 16 species recorded from the Pleistocene have their nearest living relatives limited to regions farther south, while no case of the opposite kind is recorded, would at once suggest birds as temperature indices. It will be noticed, however, that at least 9 of the abovementioned species penetrate to southern latitudes where climatic conditions equal or even surpass in rigor those in the northern latitudes at which the fossils are found. Are birds good climate indicators? May not the birds have changed instead of the climate?

The bird's tendency to migrate may throw him into one particular latitude at a certain part of the year. Within a week his habitat may appear to have changed by a thousand miles north or south from that point. During these migrations much mortality occurs and bodies may be thrown upon shores of lakes or bays in large numbers and entombed before being destroyed by predaceous or scavenging species; hence they are more liable to preservation as fossils. Ephemeral conditions of food or water may attract birds from distances or the disturbance of migration waves may cause their great abundance for brief periods as "bird storms." As example consider the hawk, *Buteo swainsoni*, which in great hosts follows the grasshopper swarms in California. The writer has seen disease and accident bring down many individuals from such a flight as they seek noonday water or evening roost in gregarious fashion. A species may thus be exceedingly abundant and especially subject to agencies of entombment in the locality where it is really not a common bird.

The occurrence of the wood ibis *Mycteria* in southern California is an equally interesting case. This peculiar bird seems to exercise

an erratic northward migration in occasional years during the months of July or August, which brings it within the San Diegan Region for a few weeks only. Their remains have here been found, after the flock's departure, about the muddy sloughs formed by flowing wells. The species may thus be part of our fauna only in the hot month of July and add a very positive, tropical note which is not at all indicative of the general climate of the region.

The Rancho La Brea beds lie geographically in the midst of the present faunal area known as the San Diegan Region. The immediate vicinity is open country 10 miles from the sea and but slightly above sea-level. Drainage is slow and surface waters, during the wet season, may accumulate in ponds 10 to 50 feet in diameter—ponds which disappear as spring advances. In but few instances can seepage keep alive small patches of marsh vegetation through the year. The region is treeless except for an occasional willow or sycamore fed by underground waters of the slight depressions. The low Santa Monica mountains on the north and the fog-laden sea-breeze from south and west prevent a truly desert condition from prevailing. Changes of elevation since the Pleistocene can not have been great, though perhaps they were sufficient to bring the sea at times much nearer than it is at present.

Within the memory of the writer in southern California, such a locality has been seen to attract eagles, condors, hawks, kites, geese, herons, cranes, grebes, pelicans, in fact all the types of birds found in the Asphalt except those no longer native to Southern California. The presence of water birds' remains can not therefore be offered as evidence of greater humidity than characterizes the climate at present. Anomalies in distribution mentioned above may be summarized as follows:

| Fossil Species: | Nearest Living Relative: |
|---|---|
| Ajaia ajaja (Linnaeus). | Ajaia ajaja (Linnaeus). |
| Ciconia maltha Miller. | Euxenura maguari (Temm). |
| Jabiru mycteria (Lichtenstein). | Jabiru mycteria (Lichtenstein). |
| Parapavo californicus Miller. | Agriocharis or Pavo. |
| Catharista occidentalis Miller. | Catharista urubu (Vieillot). |
| Sarcorhamphus clarki Miller. | Sarcorhamphus gryphus auct. |
| Cathartornis gracilis Miller. | Sarcorhamphus gryphus auct. |
| Geranoaëtus fragilis Miller. | Geranoaëtus melanoleucus auct. |
| Geranoaëtus grinnelli Miller. | Geranoaëtus melanoleucus auct. |
| Morphnus woodwardi Miller. | Morphnus guianensis auct. |
| Morphnus daggetti Miller. | Morphnus guianensis auct. |
| Falco sp. | Falco fusco-cerulescens Vieillot. |
| Polyborus cheriway (Jacquin). | Polyborus Cheriway (Jacquin). |
| Neophrontops americanus Miller. | Old World vultures. |
| Neogyps errans Miller. | Old World vultures. |

In a general paper on the Pacific Coast fossil avifauna, published by the writer in 1912,[1] a somewhat extended discussion of this subject was entered into.

[1] L. H. Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, No. 5, p. 103, 1912.

Summing up the evidence of a warm, moist climate during the Pleistocene, we have the following points, all of which are inconclusive:

1. The presence of species whose nearest living relatives are at present more tropical in distribution.
2. The presence of an abundant fauna which is suggestive of a favorable climate.
3. The presence of aquatic species and of water-worn chips laid down in places now dry but showing no great changes in topography.
4. The suggestion that the mammals of Rancho La Brea were in some measure led to the region by the presence of water.

As zone determiners for the zoologist, Recent birds constitute a valuable asset because here the student is in a position to determine the species as resident, summer, winter, or transient visitor. The palaeontologist is, however, without data to determine these points in regard to a fossil species; therefore fossil remains of birds must not be used as faunal zone-determiners upon the same basis as the nearest related Recent species would serve. An entirely new set of standards will have to be set up and such will be possible only after a far more abundant fossil avifauna is known.

The question of the larger physiographic barriers as affecting distribution and diffusion from centers of origin has also received some slight contribution from palaeontology. In 1908 Gaillard[1] recorded a case of a cathartiform vulture having straggled into Europe during the Oligocene. This is the only record previous to the opening up of the Rancho La Brea beds that the writer has been able to find, where either cathartid or vulturid has crossed the great barrier of the oceans. The Asphalt beds furnish two instances of such wandering. At least two species of Old World vulturids occur in these beds, one common and the other more rare. It seems thus that both these families of rather large birds have behaved with respect to the oceanic barrier in much the same manner as have several of the large mammals in their intercontinental migrations. In both cases a family has had the virility and the adaptability to overcome the physiographic obstacle to its diffusion, yet it has survived only on one side of the oceanic barrier.

Parallel evolution in Old and New World lines of descent is interestingly displayed in the elongation of the metatarsal region of certain of the raptors of both realms. *Serpentarius* of south Africa has sacrificed entirely the prehensile function of the foot, for the purpose of becoming a stilt-walker. The phylogenetic strain of serpentarids is one of some antiquity as is evidenced by the occurrence of related forms in the Miocene of France. In the new world the same tendency seems to have cropped out at a later period. The morphnine eagles, *Morphnus* and *Geranoaëtus*, are birds of elongate tarsal segment and

[1] C. Gaillard, Ann. de l'Univ. de Lyon, n. ser. 1, Sc. & Med. Fasc. 23, 1908.

proportionately weakened foot. The extreme of this modification is seen in the extinct species *Morphnus daggetti*, lately excavated at Rancho La Brea by the Museum of History, Science, and Art of Los Angeles. This form has a shank which lacks but 4 mm. of equaling the same segment in the great blue heron, *Ardea herodias*. The distance of the papilla of the tibialis anticus muscle down the shaft indicates the power arm of the lever in flexing the tarsal joint; the total length of the bone represents the resistance arm; the ratio of these two dimensions is assumed to be a rough index of the lifting power of the raptorial foot. This ratio in *Aquila* amounts to 0.302. In the Pleistocene morphnines it sinks as low as 0.125. The very weak trochlea, set straight on the shaft of the tarsus at nearly the same level, point to an ambulatory foot instead of a predatory weapon and an organ of prehension. The conclusion is almost unavoidable that the foot of *Morphnus daggetti* is a New World parallel of the South African *Serpentarius*, a parallel thrust off from the accipitrine stock later in the ramifications of that great stem.

## RECORD OF SPECIES.

Except where especially designated, the remains here recorded are to be found in the University of California Collection of vertebrate Palaeontology and in the Los Angeles County Museum of History, Science, and Art. Sequence of the species and citation of authors of Recent species is taken from the American Ornithologists Union, Checklist of North American Birds, 1910 edition.

### PYGOPODES.

#### COLYMBIDAE.

##### Genus COLYMBUS ?.

The collection at Los Angeles contains a single humerus displaying the characteristic topography of the grebes. The size of the specimen is equal to the corresponding bone of the Recent species *Colymbus nigricollis californicus* (Heermann) or of *Podilymbus podiceps*, both of which occur in the locality to-day. The fossil might be assigned to either species on the basis of the limited material. Grebes are attracted to the locality of Rancho La Brea at the present time when, during the rainy season, ponds of water with bordering rushes accumulate in natural depressions. Mr. L. E. Wyman, while in charge of the excavations of the Los Angeles Museum, picked up one specimen of *Colymbus* that had its feathers so smeared with oil as to be completely helpless.

Shufeldt found five species of grebes more or less common in the Pleistocene of Fossil Lake in Oregon, thus proving the presence of the group in considerable numbers. The fact that a single bone represents the order in the Asphalt collections would suggest that the bodies of water accumulated in this locality, at the time of formation of the lenses, were of rather ephemeral nature.

[1] R. W. Shefeldt, Journ. Acad. Nat. Sci. Phila., ser. 2, No. 9, p. 389, 1892.

## ANSERES.

### ANATIDAE.

The remarks made in discussing the very rare grebe remains as indicating the temporary nature of the Pleistocene pools at Rancho La Brea are in no way countered by the presence of an appreciable number of anserine remains in the collections. Irrigated fields of the California farmer are visited by immense flocks of geese and ducks, during which time much damage is done by the puddling of the soil about the plant stems. Such conditions would offer no attraction to diving birds, such as the grebes. Anserine remains are, however, not of great abundance nor of great variety. This limitation of material makes final assignment to the proper species a matter of great difficulty in a group of birds showing such range of variation in size. Much of such assignment is necessarily tentative.

#### Anas platyrhynchos Linnaeus ?.

The major portion of an anserine humerus in the University collections is indistinguishable from that of a female specimen of the mallard duck from the Los Angeles region.

#### Nettion carolinense (Gmelin) ?.

An almost perfect tibiotarsus in the University collection corresponds completely with the same bone from a Recent female of this species. Other duck remains occur but are not sufficiently characteristic to be assignable to species. By far the most abundant anserine remains are assignable to the larger forms, such as the genus *Branta.*

#### Branta canadensis (Linnaeus).

The species *Branta canadensis,* as it exists to-day, is split into a number of varieties of great diversity in size, the largest being *B. c. canadensis* and the smallest *B. c. minima.* Four such subspecies have been recorded from Southern California during winter migrations, at which time there seems to be no barrier to their intermingling. Analogy with other species of large birds would suggest that the degree of variation in this species during Pleistocene time would probably have been no less and possibly would have been even greater than at present. The remains of geese from the Asphalt lenses show a great diversity of size and proportions. This diversity led at first to assignment of the remains to more than one species. Later studies of Recent skeletons in the Museum of Vertebrate Zoology has, however, made it evident that the one species *B. canadensis* might be expected to include almost the entire mass of material.

The species is by far the most common anserine in the collections. The University collections contain five typical tarsometatarsi, portions of the tibiotarsus, a perfect humerus, and a coracoid. These latter two bones reach almost swan-like proportions.

*Tarsometatarsus.*—The variability of this segment of the skeleton is observable both in the length and in the relative stoutness. One member of the series is, in fact, so markedly slender, with such small trochleae that taken by itself it would readily be considered as specifically different from *B. canadensis.* A table of measurements of the fossils and of Recent skeletal material is offered (in millimeters).

*Measurements of the tarsometatarsus of Branta canadensis, Pleistocene and Recent.*

| | Pleistocene. | | | | | Recent. | |
|---|---|---|---|---|---|---|---|
| Length | 86.6 | 93 | 94.9 | 94.3 | 88.4 | 93 | 78.5 |
| Diameter of head region | 89 | ...... | 18.7 | 20.3 | 16.7 | 19 | 15.3 |
| Diameter through trochleae | ...... | 20 | 19.5 | 21.4 | 17 | 18.7 | 15.7 |
| Least diameter of shaft | 7 | 7 | 7.2 | 7.9 | 6.3 | 7.4 | 6.1 |
| Diameter middle trochlea | 8.2 | 8.8 | 8.7 | 9 | 7 | 8.8 | 6.5 |

*Tibiotarsus.*—Two specimens of the distal portion of the tibiotarsus correspond perfectly in osteologic characters with the Recent birds. One specimen is slightly larger than the specimen of *B. c. canadensis* and the other fragment is intermediate in size between *canadensis* and *B. c. hutchinsi.*

*Coracoid.*—The single large coracoid in the University collections is intermediate between *Branta* and *Olor*, as shown by the following comparative table of measurements:

*Measurements of coracoid of Recent anserines with the fossil specimen from the Asphalt.*

| | Olor columbianus. | B. c. canadensis. | Fossil. |
|---|---|---|---|
| | *mm.* | *mm.* | *mm.* |
| Length head to manubrial end of sternal facet . . . | 81 | 69 | 74 |
| Transverse diameter of neck.................... | 12.8 | 10 | 10.5 |

*Ulna.*—There is very little that is characteristic about the ulna beyond the general anserine nature of the bones. Two almost perfect specimens of this segment in the University collections correspond perfectly with the Recent bird of the subspecies *B. c. canadensis.*

#### Genus BRANTA (?) sp.

The University collections contain two tarsometatarsi representing some anserine more slender than *Branta canadensis minima* and yet stouter than that large-footed tree-duck, *Dendrocygna bicolor.* The species represented was either a pigmy goose or a stilt duck, but the exact affinities are not determinable from the limited material at hand. The following dimensions of the specimen are recorded. Length, 63.8 mm.; diameter of head, 11.3 mm.

## HERODII.

### PLATALEIDAE.

#### Ajaia Ajaja (Linnaeus) ?.

The collection at Los Angeles contains specimen of the tarsometatarsus of a species not to be distinguished from the Recent roseate spoonbill. Comparison was made with a specimen from Salvador and the coincidence of the two bones is perfect. Recent birds of this species are a matter of frequent popular report and of rarer scientific record in Southern California. In view of the occurrence at Rancho La Brea of so many semi-tropic forms, the rarity of this species in the collections is interesting.

### IBIDIDAE.

#### Plegadis gaurauna (Linnaeus).

A single tibiotarsus represents this member of the Recent avifauna of the region. Except for the fracture of the proximal extremity, the specimen is perfectly preserved and displays all the characters of the Recent specimens examined. The single bone was excavated by the Los Angeles Museum at a depth of 17 feet in pit No. 67. The species to-day inhabits quite temporary ponds as well as the more permanent bodies of water. Its occurrence at the time of the formation of the deposits is without particular significance.

### CICONIIDAE.

#### Mycteria americana Linnaeus ?.

In a general list of West Coast fossil birds published in 1912[1] the wood ibis was recorded from Rancho La Brea. The record was based upon the very characteristic symphyseal region of the lower jaw in collections made by the Los Angeles High

[1] L. H. Miller, Univ. Calif. Publ. Dept. Geol., vol. 7, no. 5, 1912.

School under direction of Mr. J. Z. Gilbert. The specimen has been lost to sight, hence the record can not be reviewed in this paper with positive results. There is no doubt in the mind of the writer, however, as to the very close affinity if not the identity of this fragment with the Recent *Mycteria americana.* The significance of the occurrence is about the same as in the case of the previously mentioned species *Plegadis gaurauna.*

**Jabiru near mycteria (Lichtenstein).**

The University collections contain 4 specimens representing a stork of much larger size than *Cinconia maltha,* which latter species runs fairly constant in size. The tibial and tarsal fragments of the large species were compared with a single Recent specimen of *Jabiru* and found to be smaller than that specimen, but were assigned to the same species in spite of the discrepancy. Portions later excavated represent the coracoid, carpometacarpus, and tibiotarsus. All show similarly this intermediate size between *Ciconia maltha* and the larger *Jabiru.* An osteological difference between the Pleistocene *Ciconia* and the Recent *Jabiru* is the following. In viewing the tibial condyles from the side, a tangent drawn at the middle of the arc of curvature would form almost a right angle with the shaft of the bone in *Ciconia maltha.* The angle would be more acute in *Jabiru.* In this respect the larger species from the Asphalt can be distinguished from the smaller *C. maltha.* It can not be distinguished from the Recent *Jabiru mycteria* on the basis of the limited material at hand. A single tarsometatarsus in the collection at the Los Angeles High School measures up to the recorded lengths of *J. mycteria;* hence it would seem that the Asphalt material is simply smaller in average than the single Recent specimen that the writer has been permitted to examine.

*Table of measurements Jabiru mycteria?.*

| | *mm.* |
|---|---|
| Coracoid: | |
| Length from head to manubrial end of sternal facet | 97.5 |
| Maximum diameter of head | 23.6 |
| Transverse diameter of shaft at neck | 11.3 |
| Carpometacarpus: | |
| Maximum length | 147 |

In the collections at the Los Angeles Museum a further representation of the species makes the following data available:

| | *mm.* | | |
|---|---|---|---|
| Tibiotarsus: | | | |
| Length between proximal and distal articulations | 380 | | |
| Diameter through condyles | 20.5 | | |
| Tarsometatarsus: | | | |
| Length, intercotylar tuberosity through middle trochlea | 322 | 312 | 290 |
| Diameter through trochleae | 26 | 25.8 | 23.9 |
| Length femur head to inner condyle | | 128 | 120 |
| Least transverse shaft diameter | | 17 | 16 |

**Ciconia maltha Miller.**

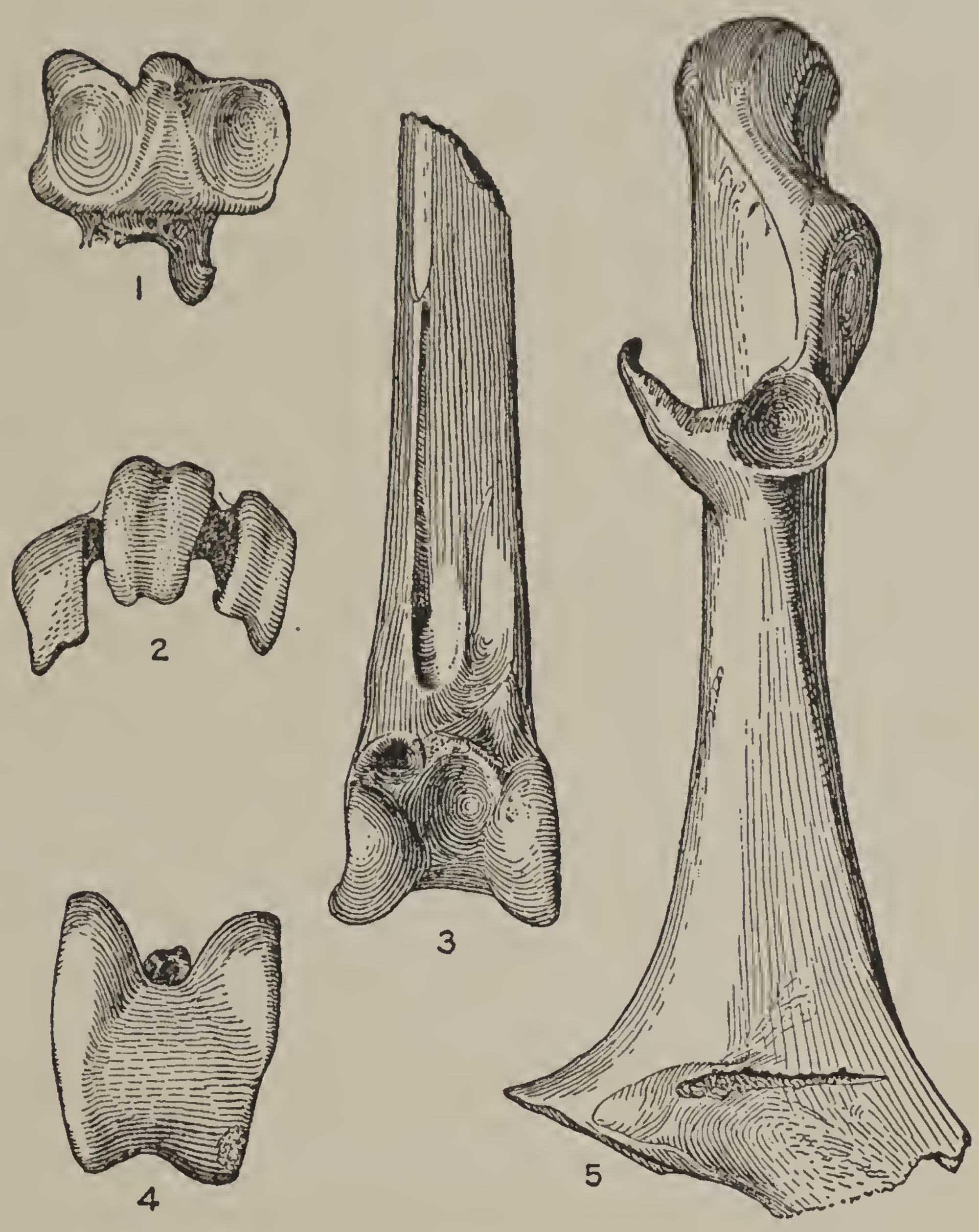
*Ciconia maltha* Miller, Univ. Calif. Publ. Bul. Dept. Geol., vol. 5, No. 30, p. 440, 1910.

*Type specimen.*—A tarsometatarsus No. 11202; cotypes Nos. 11237, 12529, 12527, 12532, and 12526, Univ. Calif. Col. vert. Palae.

This stork seems more nearly related to *Euxenura maguari* of Argentina than to any other Recent species examined. In the original description of the species comparison with *Euxenura* was made. Subsequent discoveries in the Asphalt have substantiated the results then published and have added some points regarding skeletal parts not then known. The amount of known fossil material has so increased as to include now practically all the more characteristic parts of the bird's skeleton. Parts thus added to the collections include humerus, ulna, carpometacarpus, femur, sternum, and skull. Differences noted in comparison with *Euxenura* may be summarized as follows:

Size slightly in excess of *Euxenura.* Tarsometatarsus less robust; trochleae relatively slender; hypotarsus set lower upon the posterior aspect of the bone; inter-

cotylar tubercle, as seen from in front, more distinctly set off from the head. The distal end of the tibiotarsus shows a different curvature of the condyles, such that the chord of the arc, discerned in viewing the bone from the side, passes almost at right angles to the axis of the tibia. Coracoid less flattened, more gradually tapering from the expanded base; sternal facet wider; head longer as measured from the scapular fossa.




*Ciconia maltha.*
FIGS. 1, 2.—Tarsometatarsus from proximal and from distal ends.
FIGS. 3, 4.—Tibiotarsus from front and from distal end.
FIG. 5.—Coracoid from dorsal side.

The fairly abundant remains of this stork in the Asphalt deposits must not be interpreted as indication of a greater humidity in the region than is at present encountered there. Various writers upon the habits of storks in both Old and New Worlds speak of the plains-dwelling habit of the birds, especially during insect outbreaks, such as the locust storms of Palestine and of Argentina. *Ciconia maltha* probably had much the same appetites and perhaps presented much the same appearance as does *Euxenura maguari* of the Argentine pampas to-day.

## ARDEIDAE.

Members of this avian family are surprisingly rare, both in point of variety and of numbers, a phenomenon very hard to understand. A combination of local physiographic conditions which would attract *Branta* on the one hand and *Parapavo* on the other hand would seem liable to offer inducement at some place or time to such versatile birds as the Ardeidae. The grasshoppers in dry open areas, the field mice of cultivated fields, the larvae and earth-worms drowned out by the most ephemeral irrigation waters, the marine life of great kelp beds clinging to submerged reefs off

shore—these all offer attractions to herons. The Recent *Nycticorax* is not an infrequent victim of the leakage outpours of the oil fields to-day. Why are herons so infrequently met with in the Pleistocene lenses of Asphalt? As a matter of fact they are among the rarest of Rancho La Brea birds.

*Measurements (in millimeters) of Ciconia maltha in comparison with Euxenura maguari.*

| | Fossil specimens. | | | | Euxenura. |
|---|---|---|---|---|---|
| Tarsometatarsus: | | | | | |
| Total length | 275 | 292 | 278 | 310 | 267 |
| Transverse diameter of head | 22 | 22.8 | 22 | 22.8 | 24 |
| Transverse diameter of foot | 25 | 25 | 24.5 | 26 | 24.7 |
| Transverse diameter of shaft | 9 | 8.8 | ........ | 10 | 9.5 |
| Tibiotarsus: | | | | | |
| Length from peronial condyle | 312 | ........ | ........ | ........ | ........ |
| Transverse diameter of head | 24.3 | ........ | ........ | ........ | ........ |
| Transverse diameter of condyles | 18.7 | 19 | 18.3 | ........ | 19.1 |
| Transverse diameter of shaft | 11.1 | 10.4 | 10.4 | ........ | 10.1 |
| Femur: | | | | | |
| Length over trochanter and outer condyle | ........ | ........ | ........ | 116 | 117 |
| Greatest transverse diameter of proximal end | ........ | ........ | ........ | 31 | 28 |
| Greatest transverse diameter of distal end | ........ | ........ | ........ | ........ | 30 |
| Transverse diameter of shaft | ........ | ........ | ........ | 15 | 15 |
| Sagittal diameter of shaft | ........ | ........ | ........ | 13 | 12.6 |
| Humerus: | | | | | |
| Length over all | ........ | ........ | ........ | 250 | 225 |
| Transverse diameter through distal condyles | ........ | ........ | ........ | 37 | 34.8 |
| Least transverse diameter of shaft | ........ | ........ | ........ | 17 | 16 |
| Least sagittal diameter of shaft | ........ | ........ | ........ | 14.5 | 13.3 |

### Ardea herodias Linnaeus.

The great blue heron is known from specimens in both the University and the Los Angeles collections. The tarsometatarsus, the tibiotarsus, and the coracoid are represented by material indistinguishable in osteological characters from that of the Recent species from the same region.

### Botaurus lentiginosus (Montagu) ?.

The distal end of a tarsometatarsus and a coracoid in the collections of the Los Angeles museum represent a bittern which is indistinguishable from the Recent species of the region. The fossil material is meager and so incomplete that the assignment to species is made with some reservation.

## PALUDICOLAE.

## GRUIDAE.

### Grus minor Miller.

*Grus minor* Miller Univ. Calif. Publ. Bul. Dept. Geol. vol. 5, No. 30, p. 446, 1910.

In an earlier paper on the wading birds of the Asphalt, *Grus minor* was described as a new species including all the material at that time known from the Asphalt. For comparison with the fossil material there was available a complete skeleton of a Recent bird labeled *Grus canadensis*. The Pleistocene material was markedly smaller than this so-called *G. canadensis* and showed certain osteological differences as well. The species *Grus minor* was established to include the fossil material and was published as the smallest of the North American cranes. Since the publication of those studies,

there have come to hand specimens in the flesh and prepared skeletons from the California Museum of Vertebrate Zoology which are unquestionably *Grus canadensis.* Examination of this material makes it clear that an error was made in the labeling as *G. canadensis* of the Recent skeleton used for comparison in establishing the Pleistocene species *G. minor.* That such error could creep into the labeling of a considerable collection of osteological material is probably due to the way in which skeletal material is often collected. Many specimens from large zoological parks arrive at the preparation rooms of the taxidermist in a poor state of preservation, with plumage worn and soiled from sickness in captivity. The specimen is discarded as a mount or a cabinet skin and the least skilled of many assistants is directed to rough out the skeleton. After removal of the plumage, a bird's identity is not easily determined. Thus the name of an American species may be attached to a bird of moderate size from India or other distant section of the globe. Such errors may then occur in some otherwise very valuable osteological collections and the reader's forbearance is invoked in order that attention may be called to a danger which resulted in confusion regarding the fossil gruids from Rancho La Brea.

Only one specimen of *Grus mexicana* was available for comparison in the review of the cranes. In *G. mexicana,* the tibiotarsus is larger than in the type of *G. minor* and displays marked differences in the proportion of ectocondyle to entocondyle. *Grus minor* averages larger than any of the specimens of *G. canadensis.* Osteological distinctions, noted in the original description, fall to the ground on comparing the fossil bird with true *G. canadensis,* and the validity of the species *G. minor* becomes questionable. The series of material both Recent and fossil is so limited that the final word on the relationships of the various gruids can not be pronounced, but the indications are that *Grus minor* is a species intermediate in size between *G. canadensis* and *G. mexicana.*

Since this manuscript went to press, later study announces this species as invalid.

*Table of measurements (in millimeters) of Grus canadensis and G. minor.*

| | G. canadensis. | | | G. minor. | | |
|---|---|---|---|---|---|---|
| Tibiotarsus: | | | | | | |
| Transverse diameter of condyles | 17.3 | 17.5 | 17.3 | 21.3 | 22 | 18.8 |
| Sagittal diameter of condyles | 15 | 17.4 | 15.9 | 20.5 | 21.5 | 17.9 |
| Depth of ectocondyle | 10.5 | 12.3 | 11 | 13.8 | 14.5 | 12.3 |
| Depth of endocondyle | 7.6 | 9.0 | 7.8 | 11.2 | 10.5 | 8.3 |
| Tarsometatarsus: | | | | | | |
| Maximum length | 175 | ........ | 191 | 223 | ........ | ........ |
| Transverse diameter of head | 19 | ........ | 20 | 26.4 | ........ | ........ |
| Transverse diameter of foot | 19 | ........ | 19.2 | 23.4 | ........ | ........ |
| Transverse diameter of shaft | 66 | ........ | 7 | 9 | ........ | ........ |

## Grus near americana (Linnaeus).

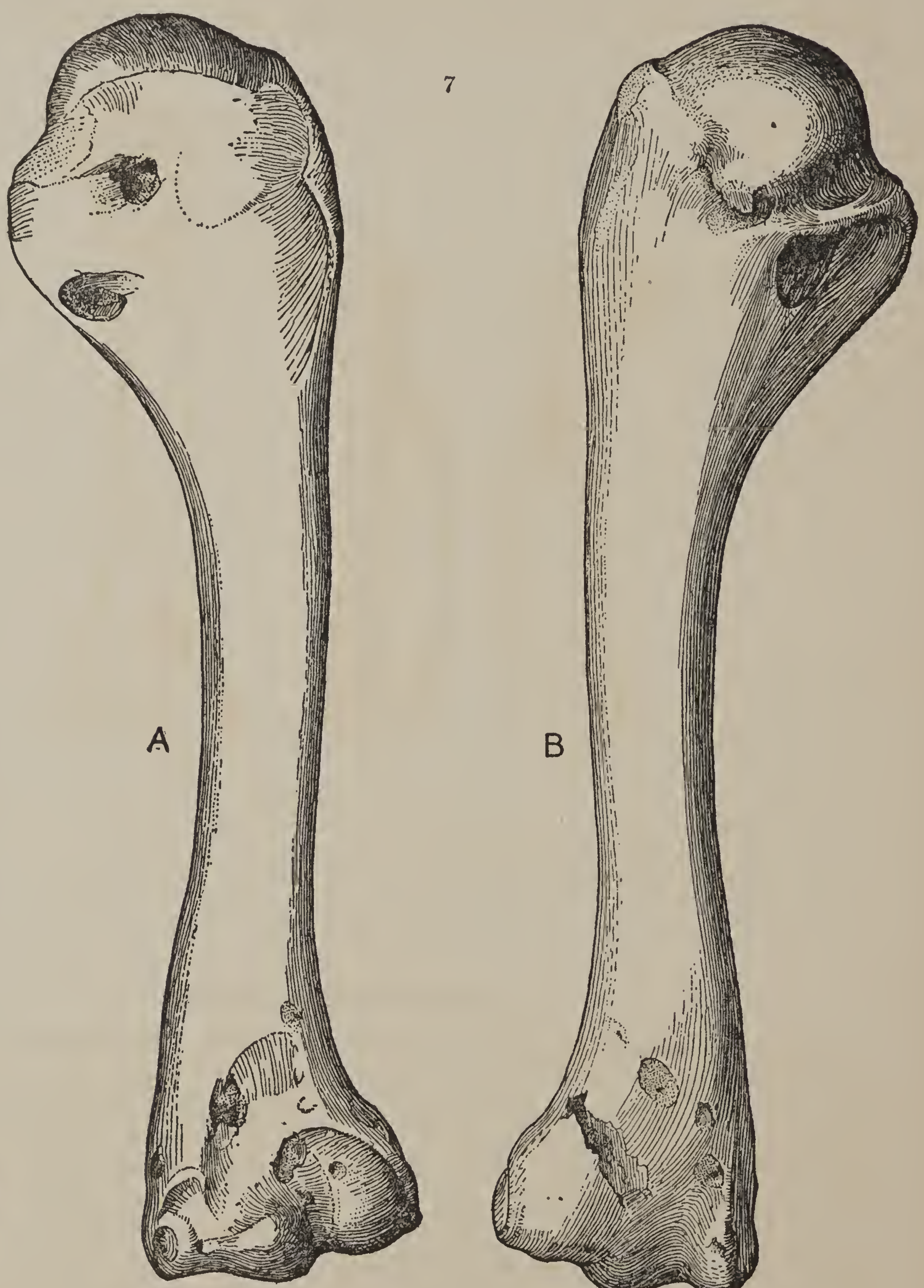
Despite the recognized variability of many Pleistocene birds it seems scarcely proper that all the Rancho La Brea gruid remains should be assigned to a single species. Possibly the remains assigned to the species *minor* are really not homogeneous. It may be, however, asserted that a larger species is represented as well. There occur in the University collections several specimens which pertain to a species of crane equal to or larger than *Grus americana* or the oriental *G. antigone.* A single specimen each of the last two species mentioned is at hand and both are exceeded in size by the Rancho La Brea bird. The fossil material includes the sternum, a perfect coracoid, and a perfect carpometacarpus. The discrepancy in size is not so great as to necessarily exclude the fossil material from the Recent species *G. americana.*

*Measurements (in millimeters) of G. near americana.*

| | |
|---|---|
| Coracoid: | |
| Length from head to manubrial extremity of base | 78.7 |
| Right to left diameter of neck | 16.7 |
| Carpometacarpus: | |
| Length over all | 115.7 |
| Tibiotarsus: | |
| Transverse diameter through condyles | 25.6 |
| Sagittal diameter through condyles | 24.5 |
| Depth inner condyle | 11.8 |
| Transverse diameter of shaft | 12.3 |
| Sagittal diameter of shaft | 10.7 |

6

7




*Parapavo californicus.*

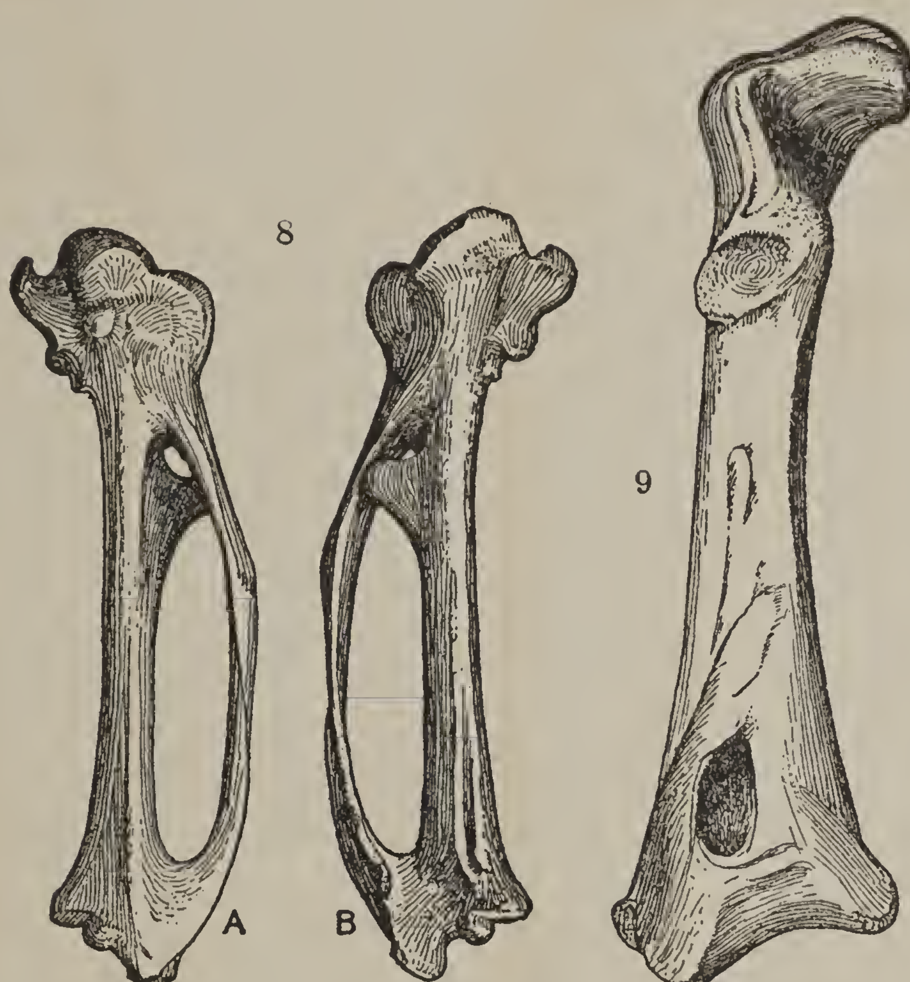
Fig. 6.—Tarsometatarsus of female. Approximately natural size.

Fig. 7.—Humerus of male. Approximately natural size. From specimen in Museum of Palaeontology, University of California. *A*, Ventral aspect; *B*, Dorsal aspect.

## LIMICOLAE.

The combined collections from the Asphalt contain not more than a good half-dozen specimens representing this great group, a fact that is especially surprising in view of the considerable numbers of other water-loving birds found there. Plover, avocets, stilts, and willets frequent the most ephemeral pools in the San Diego region to-day and even in the meager Recent oil seepages, the unrecognizable remains of shore birds in feather have been seen, yet for some reason the bones of Limicolae are almost absent from the collections.

The few specimens preserved are so diverse and the group represented is so replete with species of approximately the same size that no specific identification of the scant material is hazarded. The humerus, coracoid, and tarsometatarsus are segments of the skeleton preserved.




*Parapavo californicus.*

Fig. 8.—Carpometacarpus. Approximately natural size. *A*, Ventral aspect; *B*, Dorsal aspect.

Fig. 9.—Coracoid. Approximately natural size. Dorsal aspect.

## GALLINAE.

### PHASIANI.

**Lophortyx californica (Shaw) ?.**

Among the collections at the University and at the Los Angeles Museum, there occur very sparingly the remains of a quail, indistinguishable from the species living to-day in the region. The reservation in assignment of the remains to the species *L. californicus* is due to the fact that the unassociated bones of that species are not to be distinguished from those of *L. gambeli*, a bird of the more desert portions of the Southwest. The characteristic limb bones both anterior and posterior are represented.

The chief point of interest in the remains is their extreme rarity. The California quail is abundant to-day along water-courses through quite open country as well as in the more broken ground of foothills. There appears nothing in the bird's habits that would render it immune to the danger of the Asphalt outpours that so fatally attracted its larger relative, *Parapavo*.

### Parapavo californicus (Miller).

*Pavo californicus* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 5, No. 19, p. 285, 1909.
*Parapavo californicus* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 9, No. 7, p. 96, 1916.

Occasion has been taken but recently to review the entire matter of the relationships of the California peacock (1916) and at that time the genus *Parapavo* was established for reception of this Pleistocene species which in osteological characters seems to occupy a position intermediate between Old and New World forms. Since publication of that review, no additional light has been shed upon the situation. Examination of the collections at Los Angeles has emphasized over and over again the great abundance of the species, as well as the fact that, except for the extremely rare *Lophortyx*, it alone represents the great order of the Gallinae. In view of the great diversity shown among large raptors and the intimate connection of the Pleistocene fauna with more southerly faunas of to-day, this almost solitary example of the terrestrial fowl becomes even more striking. Careful search was made for the chacalacas of Mexico with their abundant relatives (Cracidae) but without other than negative results. The great ecologic field open to gallinaceous birds seems to have had almost a solitary tenant.

## COLUMBAE.

Comment has been made by the present writer[1] on the absence of columbine birds from all geologic horizons at that time known in America. Among the many thousands of specimens examined since that comment was published three specimens have come to light which represent the widely distributed order of the pigeons. There appears no reason for such scarcity of remains except rarity of the species in the locality at the time of deposit. Recent columbines seem particularly subject to the attractions at Rancho La Brea. Pleistocene pigeons would surely have been equally susceptible.

### Columba fasciata Say.

A single humerus in the Los Angeles collection represents a pigeon indistinguishable from the Recent species.

### Zenaidura macroura (Linnaeus).

Two specimens in the Los Angeles collection represent a species the size of the Recent mourning dove.

## RAPTORES.

The final word upon the Rancho La Brea birds will of necessity include a reiteration of the first—namely, the abundance of raptorial birds is almost incredible. Thousands upon thousands of specimens have been examined during the past seven years with the same result from each shipment of unassorted material: raptores constitute the great majority both of individuals and of species. The present-day ornithologist is more or less accustomed to thinking of water fowl, of fish-eating birds, or of the gregarious passerines in terms of large numbers, but to find the remains of condors, eagles, and hawks in such limitless numbers is a continued surprise. It also emphasizes anew the unusualness of the method of entrapment, comment upon which has been repeatedly made by writers upon the subject of the Asphalt deposits.

Richness of the mammalian fauna of the time had no doubt some bearing on the number of large raptors, although *Parapavo* probably

[1] Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, No. 5, p. 101, 1912.

paid substantial tribute to this voracious host. The proportions of large species to smaller, as indicated by their remains in the Asphalt, can not be considered as indicating the true condition of affairs at the time. Small birds have been less attracted or have been less commonly preserved. The fact remains that the number of individuals representing the owls, hawks, and falcons is small as compared with the number classed as eagles and vultures.

As to the comparative abundance of the larger species, the numbers of their remains probably show the approximate truth as regards relative abundance of the species composing the fauna of that time. The element of susceptibility to the attractions of Rancho La Brea may play some part in the drama. *Haliaëtus*, for example, is to-day a more piscatorial bird than is *Aquila*, even approaching in this respect the habits of the osprey. Such habit may have prevailed during the Pleistocene and would well account for the relative scarcity of *Haliaëtus* remains in the Asphalt beds. Such aggressive falcons as *Falco mexicanus* occur but rarely in the collections, yet its still feathered remains have been found in the outpours of waste oil from the pumping stations in the oil fields. Its noble nature seems to have been susceptible to the temptation there. Possibly this raptor was relatively rare in the region at the earlier time.

One of the most abundant of the smaller raptors in all the collections is *Polyborus*, a fact not at all surprising after the truth of its presence at this latitude has once been established. The ambulatory gait of the bird, together with the reprehensible feeding habits, render the species particularly susceptible to the Asphalt trap. Its relative abundance also was probably great as, in tropical countries to-day, the scavengers commonly outnumber the actively predatory forms. *Neophrontops* probably occupied much the same ecologic position as did *Polyborus*. Remains of the former are slightly less abundant than those of the latter, but the disparity is not great. The morphnine eagles are rare, the Daggett eagle being known from but five specimens.

## CATHARTIDAE.

### Gymnogyps californianus (Shaw).

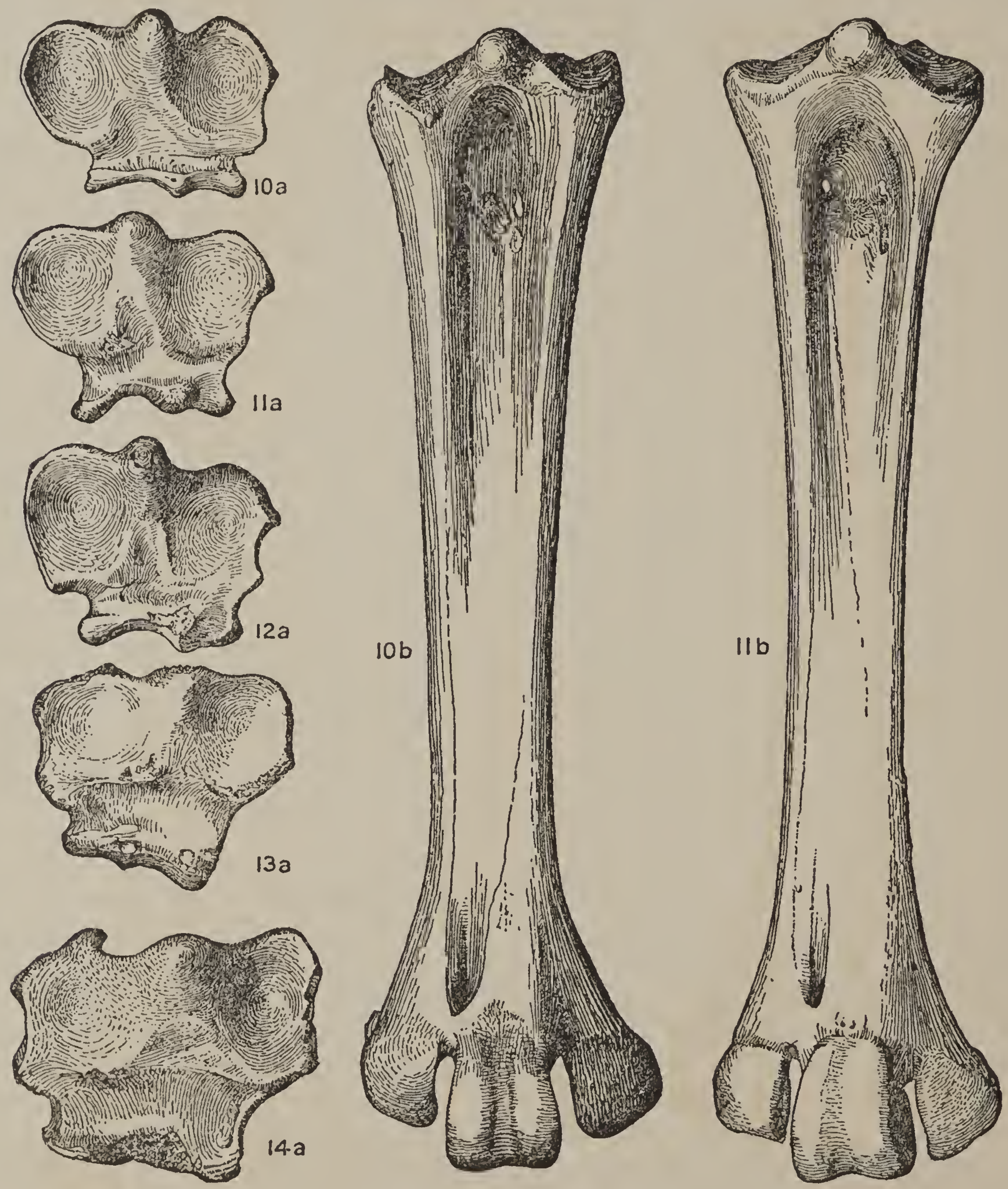
This species is the most abundant cathartiform in the Asphalt deposits and stands second only to *Aquila* in point of numbers. The almost incredible masses of its remains lend somberness to the picture one's imagination paints of the drama enacted about the Asphalt trap. The remains have been scrutinized carefully to note degrees of variability, such as characterize *Haliaëtus*, *Bubo*, and *Cathartes*. The continued surprise is that so large a bird is subject to so limited a degree of variability. Long series of the same skeletal segment display a remarkable uniformity in size. Young birds are less robust of limb bones, though the size of the articular surfaces in juvenals seems to equal that in adults. Study of such extended series of this species helps to throw into contrast the very few specimens which constitute the only remains of the other two Rancho La Brea condors. *Sarcorhamphus clarki* and *Cathartornis gracilis*.

Additional material of the Recent species but adds to the earlier conclusion that the Pleistocene phase of *Gymnogyps californianus* is osteologically identical with the Recent phase.

**Sarcorhamphus clarki L. H. Miller.**

*Sarcorhamphus clarki* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 1, p. 11, 1910.

In the collections at the Los Angeles Museum 3 specimens of the tarsometatarsus of this species were found. These substantiate the characters recorded in the original description of the type. Particularly noticeable are the approach to a cylindrical form of the shaft and the large size of the toes as indicated by the trochleae. The possibility of such differences being due to youth of the individual is practically eliminated by the fact that the Los Angeles specimens are larger than the type and show complete ossification of the various parts. The rarity of the species in the asphalt collections is without doubt in direct proportion to its numbers in the region at that

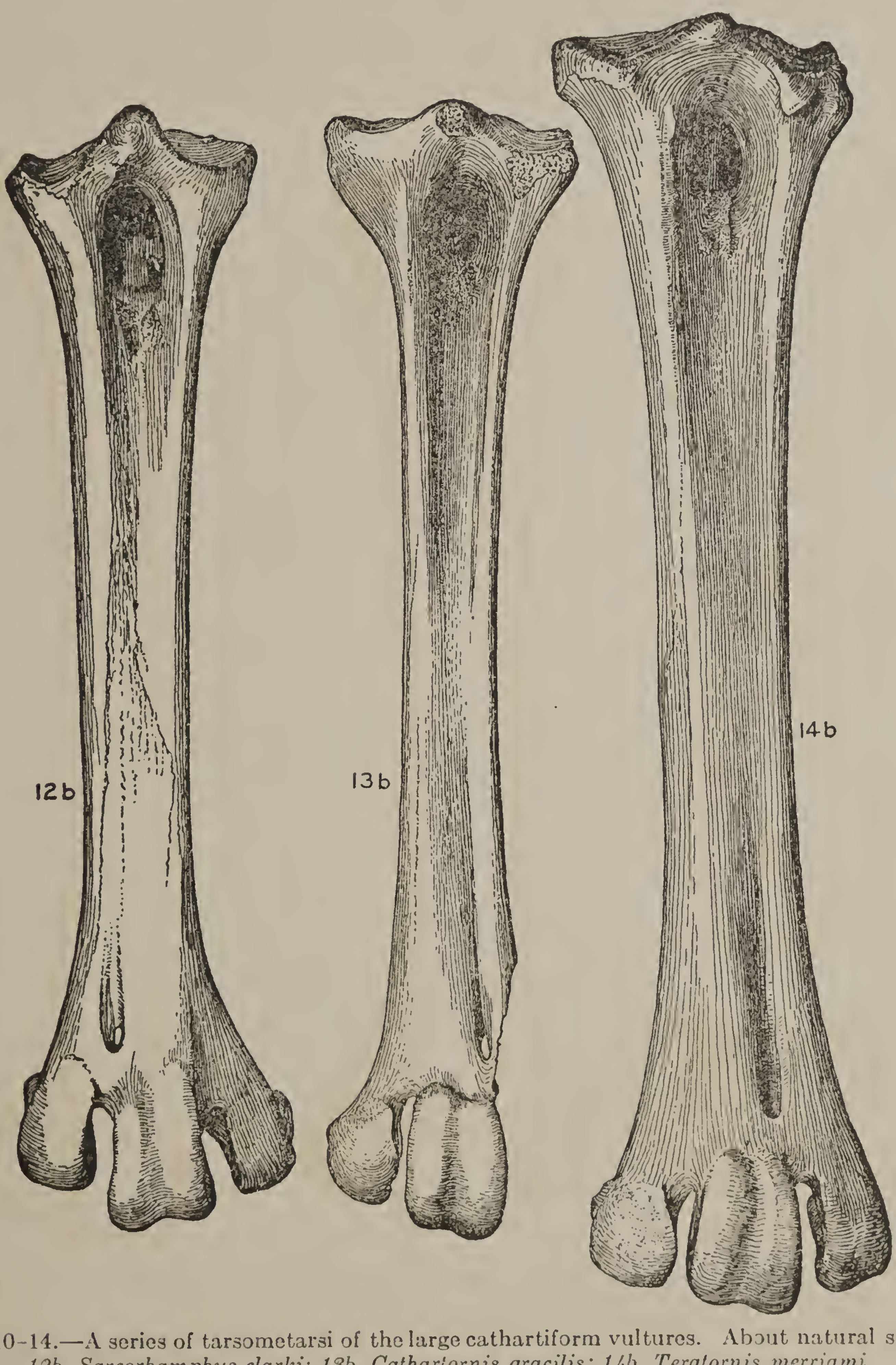



Figs. 10–14.—A series of tarsometarsi of the large cathartiform vultures, about natural size. 10*a*–10*b*, *Gymnogyps californianus;* 11*a*–11*b*, *Sarcorhamphus gryphus;* 12*a*, *Sarcorhamphus clarki;* 13*a*, *Cathartornis gracilis;* 14*b*, *Teratornis merriami.*

time. Possibly the few individuals entrapped were stragglers from a more densely populated area corresponding more nearly with the habitat of the living *Sarcorhamphus gryphus* of the South American continent.

The following description, quoted from the original paper, gives the comparison of tarsometatarsus of *Sarcorhamphus clarki* with that of *S. gryphus.*

"The two bones are almost identical in length, which makes comparison easier. The view of the two specimens from the anterior side shows the fossil form to differ from the Recent in the following details: The inner cotylus is raised farther above the outer one, the intervening tuberosity is larger and more globular. The diameter of the shaft contracts more suddenly just below the head. The excavation of the shaft in the




Figs. 10–14.—A series of tarsometarsi of the large cathartiform vultures. About natural size. *12b, Sarcorhamphus clarki; 13b, Cathartornis gracilis; 14b, Teratornis merriami.*

head region is more abrupt and more restricted. The partition separating the two proximal foramina is not more than two-thirds as wide. The attachment of the tibialis anticus blocks the whole anterior furrow which is continued down the shaft on a shallower level to disappear entirely before reaching the middle point of the shaft. The narrowest point of the shaft is at or above the middle point instead of below it. The actual width of the shaft is markedly less. The foot is narrower, the trochleae are longer but more slender.

"Seen from the outside, the tuberosity appears more knob-shaped. The hypotarsus is placed higher and its outer ridge is less pronounced. The lateral margin of the outer cotylus drops downward and forward more abruptly. The shaft from this aspect is appreciably thicker throughout its length. The outer trochlea appears less stubby.

"When viewed from the tibial end, the greater anteroposterior diameter of the head is noticeable. The inner cotylus is larger and its greatest diameter lies in a plane more nearly parallel to the sagittal plane."

### Cathartornis gracilis Miller.

(See Plate 5.)

*Cathartornis gracilis* Miller, Univ. Calif. Publ. Bull. Dept. Geol. vol. 6, No. 1, p. 14, 1910.

Besides the type and cotype of this species, both tarsometatarsi in the University collection, the collections at Los Angeles comprise two specimens practically identical with those at the University. In addition to this limb segment, several other parts of the skeleton are assigned to this species, including a fragmentary beak in the University collection and a perfect tibiotarsus, skull, and carpometacarpus at Los Angeles. The tibiotarsus is assigned to this species because it carries out the effect of slenderness seen in the tarsometatarsus. The beak certainly is not that of *Sarcorhamphus*. It differs from the beaks of the stouter-legged condors in the same way that the beak of *Catharista* differs from that of the stouter-legged *Cathartes*. One is not justified in carrying too far such an analogy of beak and foot, but in the absence of opposed evidence analogy may be added to the limited positive evidence to encourage the step which offers least confusion.

*Tarsometatarsus.*—An account of this bone is quoted from the original description as follows.

"The bone is distinguishable at a glance from that of other condors by its extreme slenderness. The total length exceeds that of any of the specimens referred to *Gymnogyps californianus*, but its shaft is actually very much narrower. Unlike the modern condors, the shaft remains nearly uniform in diameter until very near the head, where it suddenly expands. This expansion to the head is, however, mainly on the inner side, a condition which throws the center of the head far to the inner side of the axis of the shaft and gives this end of the bone a markedly goose-like appearance. The intercotylar tuberosity is very low and flat with gradual slopes in all directions. It has scarcely half the development seen in the modern condors. The excavation of the shaft just below the head is deep and almost perfectly elliptical. The attachment of the tibialis anticus appears as a pair of distinct papillae, below which the trough in the shaft is deep and almost U-shaped in cross-section. The edges of the trough are thus converted into very narrow ridges. The trough continues down the shaft to merge into the distal foramen. * * * The shaft widens very gradually to the foot and the two sides are very nearly symmetrical in curvature. This condition is in marked contrast with the asymmetry of the proximal end and with the condition in the foot of *Sarcorhamphus* and *Gymnogyps*. The trochleae are much more slender than in the existing condors. * * * A view of the proximal articular surface brings out some very characteristic features of the species. The tuberosity is scarcely evident from this direction, the outer cotylus is but little if at all in arear of the inner one and both areas have their longest axes almost parallel with the sagittal plane. * * * The inner ridge of the hypotarsus projects backward almost twice as far as does the outer

one and the inner margin of the hypotarsal 'block' has the appearance of having been thrust over toward the outer side."

*Tibiotarsus.*—The single specimen of this bone assignable to the species under discussion was found in the matrix carved from the walls of pit No. 3 of the Los Angeles Museum excavations. The specimen is at once recognizable by its great length and slenderness. It is 26 mm. longer than the corresponding segment of an adult male *Gymnogyps*, yet it is actually less in transverse dimension. In comparing the two bones osteologically, certain differences at once become apparent. Seen from the inner aspect, the shaft is less sharply set off from the condyles. This condition results in a complete concealment, from this point of view, of the supratendinous bridge and the deeper placement of the gorge underneath this bridge. At the proximal end of the bone the anterior tibial crest is more prominent and the external tibial crest is more compressed than in any of the Recent condors available for comparison.

*Skull.*—Thus far, among all the material studied in the Rancho La Brea collections, but one cranium has been recognized that could be assigned to *Cathartornis.* The cranium, rostrum, carpometacarpus, and tibiotarsus were found associated in the same section of a lens excavated by the Museum of History, Science, and Art. One other rostral fragment occurs in the Museum's collections. The only other material known to the writer was a perfect rostrum taken from these beds by the Los Angeles High School but later unfortunately lost to science. *Cathartornis* thus stands as one of the very rare species of the Pleistocene avifauna. For comparison in this study, specimens of all the Recent cathartids are available and a goodly series of specimens of the fossil phase of *Gymnogyps californianus.*

The Pleistocene *Cathartornis* differs more widely from the Recent condors than these two birds differ from each other. Comparison is here made with the Recent *Gymnogyps.*

The entire cranial mass exhibits a degree of flattening and broadening that is recognizably distinct from the high rounded dome of the condor skull. The cranial capacity is appreciably greater and the foramen magnum larger, thus indicating a bird of distinctly greater proportions than either of the modern condors, an impression further carried out by the associated metacarpus and tibia.

As seen from above, the main distinctions from *Gymnogyps* lie in the poorer development of the cerebellar region, the flattening of the dome, and the narrowing of the region between the eyes. Seen from the rear, there is noticeable the greater foramen magnum, wider and less knob-shaped postauditory processes, and a broader angle between the processes of the basioccipital region. There appear no especial peculiarities on the ventral aspect of the cranium, the basipterygoidal processes are broken away and the sphenoidal rostrum is badly fractured. There is indicated, however, a large interorbital foramen.

The characters most distinctive of the skull lie in its facial region. The whole rostrum is narrowed and extended until this portion of the skull exceeds that of the California condor by fully 25 per cent. The terminal hook is distinctly marked off from the elongate and depressed internareal region, much as is seen in the beak of *Catharista.* The nareal opening is fully twice the length of that in the Recent condors, but the ultranareal portion is proportionately much shorter. The combined result is in effect a gigantic model of the beak of *Catharista* with a strong tendency toward the spatulate.

The following are measurements (in millimeters) of skull of *Cathartornis*:

| | |
|---|---|
| Length from cerebellar prominence to beak tip | 203 |
| Transverse diameter dorsal to the masseteric area | 57.5 |
| Depth through sphenoidal rostrum to summit of dome | 43 |
| Length from rostro-cranial articulation to beak tip | 121.5 |
| Length of nareal opening | 55 |
| Widest portion of rostrum | 27 |
| Narrowest point between nostrils | 25 |
| Depth of beak between nostrils | 15 |

The following measurements (in millimeters) of rostrum of *Cathartornis gracilis* were taken from the Los Angeles specimen before it was lost to sight.

| | | | |
|---|---|---|---|
| Total length from frontal articulation.. | 110.2 | Depth at middle point of nostrils..... | 14.1 |
| Width at frontal articulation........... | 27 | Length of nareal opening............ | 50.3 |
| Width at distal end of nostrils........ | 26 | Greatest depth of nostril............. | 9.5 |
| Least width of internareal bridge...... | 5.6 | | |

### Cathartes aura (Linnaeus).

The earlier excavations by the University of California brought to light the remains of a number of individuals of this species. Very characteristic parts, such as the rostrum, shank, upper arm, and coracoid, were represented, so there can be no question as to the identity of the remains. Early publications on the birds of the deposits, therefore, listed *Cathartes* as a common bird. However, in all the extensive later excavations by the University and by the Los Angeles Museum the remains of *Cathartes* are extremely rare. That *Cathartes* is not immune to the attractions of the place is amply proven by the presence of its remains in abundance in masses of asphalt which are undoubtedly of Recent age. The only logical conclusion regarding the species is that it was extremely uncommon in this locality during Pleistocene time.

Study of these rather scant remains shows a size variation of considerable magnitude and abruptness in the series of tarsometatarsi. The series is not extensive enough to warrant a positive statement regarding the specific homogeneity of the remains. Two specimens of the fossil series, one a young bird and one a bird beyond maturity, are of pigmy size. Four Recent specimens were used for comparison and one of these birds is a juvenal. Still the unbridged gap in size appears. Studies of *Haliaëtus* and of *Bubo* show that the Pleistocene phase of a species is often subject to somewhat greater range of size variation than is the persisting phase. In the light of such studies, it may be said that during the Pleistocene, *Cathartes* was represented either by two species or by a single species more variable in size than the Recent *Cathartes aura* of the same locality.

### Catharista occidentalis Miller.

*Catharista occidentalis* Miller. Univ. Calif. Publ. Dept. Geol., vol. 5, No. 21, p. 306.

Although numberless specimens of this species have been examined from the various Asphalt collections, it has not been possible to examine further skeletal material of Recent *Catharista urubu*, hence the comparison of the fossil species with its nearest living relative has not been improved upon. Added information has been rather in the matter of relative abundance of the species. At the time that study of the first Asphalt collections was made public, *Catharista* was thought to be of about equal abundance with *Cathartes*. Subsequent and deeper excavations prove it to be by far the more abundant of the two smaller vultures. Its numbers about equal those of *Gymnogyps* or of *Parapavo* which in turn are exceeded only by *Aquila*.

The fossil *Catharista* was remarkably like the Recent bird, the differences being not visibly adaptive and therefore not probably involving a difference in habits of the birds.

A synopsis of differences between *Catharista occidentalis* and *Catharista urubu* shows that the fossil bird is larger of body as judged by the skull, sternum, and pelvis. The femur is longer by 7 per cent, the tarsometatarsus is shorter by 6 per cent, but stouter by 9 per cent; the foot is wider by 16 per cent; the humerus is longer by 8 per cent.

## TERATORNITHIDAE.

### Teratornis merriami Miller.

(See Plates 1 to 4.)

*Teratornis merriami* Miller, Univ. Calif. Pub. Bull. Dept. Geol., vol. 5, No. 21, p. 307, 1909.
*Pleistogyps rex* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 1, p. 16, 1920.

At the time the original description of this interesting species was written, some question was conceded as to the propriety of ascribing the various parts of the pectoral arch to the same species as the type specimen of *Teratornis*, the skull. The probability of error recedes to the vanishing point before the repeated occurrence of the parts together in the matrix and the continued absence of other possibility. *Teratornis* is now known in this way practically beyond question except for such minor parts as the mandible, ribs, certain vertebrae, and the phalangeals. So like the condors is the great bird in less specialized portions of its skeleton that there is still question as to identity of vertebrae and toes. As thus far worked out, the foot of *Teratornis* does not differ materially from that of the condors.

*Skull.*—Later excavation has not added materially to our knowledge of the cranial portion of the skull nor has it dulled appreciation of the remarkable features of this erratic bird. The outward and backward thrust of the post-auditory regions must have added enormously to the gape. This with the very low brain case and the well-defined basipterygoidal processes and large foramen magnum gives a very positive struthious appearance and suggests a low order of mentality. An account of the oestological characters of the cranium is quoted from the original description.

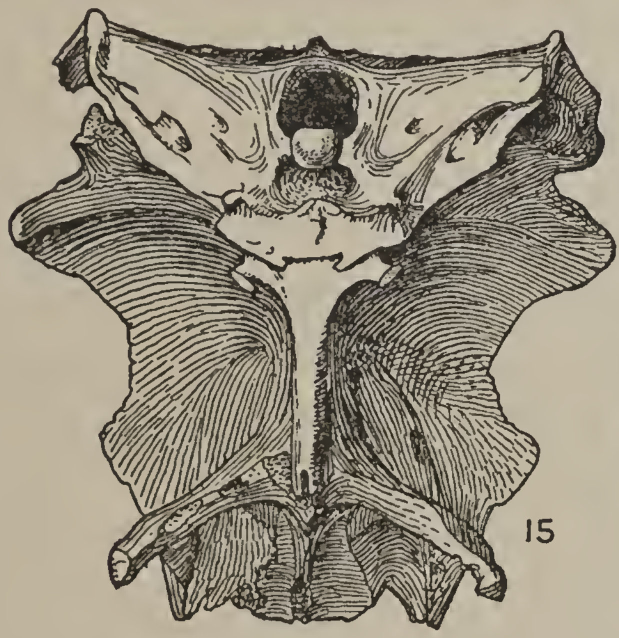

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Fig. 15.—*Teratornis merriami*. Skull. Ventral aspect. × about one-half.
Fig. 16.—*Teratornis merriami*. Skull. Occipital aspect. × about one-half.

"On viewing the skull from below at right angles to the basi-sphenoidal rostrum, two very striking characters are evident. The cerebellar region is greatly reduced and the postauditory prominences are thrust backward and outward until their ventro-lateral angles form the posterior extremities of the skull. The rear profile becomes concave in general, with the middle portion of the arc slightly interrupted by a gentle convexity. The foramen magnum seems unique among known raptors. It lies in a plane facing as much backward as downward and is decidedly deeper than wide. It has a sagittal diameter of 14.3 mm. but measures only 11 mm. across its center. Toward the condyle it widens out slightly, so that it appears bluntly pear-shaped in outline. The occipital condyle shows no peculiarity except possibly less tendency to form a constricted neck than in most raptorial birds. Just forward of the condyle, however, the basioccipital bone is excavated in two deep, rounded pits separated by a low median

ridge. In front of this depression the basisphenoid rises in an abrupt transverse ridge ending laterally in a pair of high basisphenoidal processes. The whole region immediately anterior to the condyle thus presents a very rugged topography. The basipterygoid processes are well-defined fungiform structures placed far back on the sphenoidal rostrum. This rostrum is intact and the interorbital septum is imperforate except at the optic foramen.

"The occipital region when viewed from the rear is seen to be marked by a well-defined transverse ridge passing across from one postauditory prominence to the other, and curving gently upward to form the dorsal border of the foramen magnum. This transverse ridge is the angle of intersection of two slightly concave surfaces, a postero-dorsal and a postero-ventral slope. The ventral slope, trending forward and downward, includes the plane of the foramen magnum and a nearly smooth exoccipital surface on either side of it. The whole postero-ventral surface is remarkably uniform in its concavity and almost unbroken except as interrupted near its center by the abrupt rise of the occipital condyle and by the basioccipital depressions. Above the transverse ridge the postero-dorsal area slopes forward and upward to a limiting transverse intermuscular ridge near the dorsal profile of the skull. * * * The lateral terminations of this ridge are almost confluent with the temporal crests. Thus the whole posterior aspect of the skull must have been hidden by the powerful musculature of the head and neck. * * * The masseteric depressions lie largely upon the top of the head in a plane approaching the horizontal. In Cathartidae and in Falconidae these areas lie in the lateral and posterior aspects of the skull and in a more nearly vertical plane."

The original study of *Teratornis* necessarily left the entire nareal portion of the skull unknown except for the most conservative possible restoration. Since that time the excavations by the Museum of History, Science, and Art have brought to light some almost perfect material representing the entire skull except for the palatines, pterygoids, and the quadratojugal bars. However, the anterior stubs of the palatines are present so that their relation to the maxillaries is determinable. They are evidently separated anteriorly as in the condors. Surprising to note, therefore, is the close approximation, almost to actual contact, of the maxillopalatines and yet the fusion further dorsally of the cathartiform alinasals.

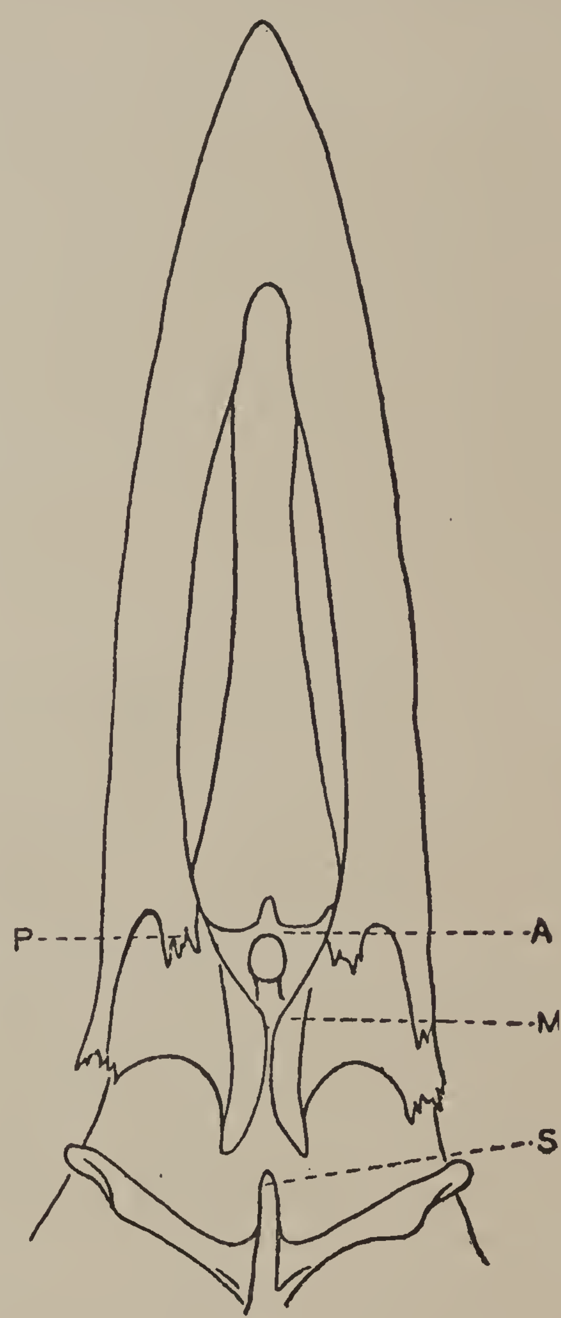


Fig. 17.—*Teratornis merriami*, rostrum, ventral view. A, alinasal; M, maxillo-palatine; P, stump of palatine; S, sphenoidal rostrum.

Another striking feature of this region is the tremendous ventral thrust of the mesial borders of the maxillaries and the consequent dorsal recession of the tomial margins of these bones. So extreme is this condition that the point of contact with the quadratojugal bar comes to lie fully a centimeter dorsal to the anterior attachment of the palatine. Even so far forward as the anterior border of the nareal opening, the tomial edge of the beak is but slightly ventral to its median plane. In the typical cathartiforms the roof of the mouth is high-vaulted transversely all the way from the terminal hook to the sphenoidal rostrum.

Absence of the quadratojugal bar makes it impossible to determine the exact angle which the rostrum forms with the skull. The indications are that this angle is intermediate between those to be noted in the cathartids and the accipitrines.

When viewed from the side, the beak presents what may be considered its weakest feature—the extreme enlargement of the nareal opening. The internareal bridge is reduced to a slender strip of bone actually less than that seen in the condor whose nareal opening is not one-fourth as deep. The same may be said with equal truth of the maxillary border of this opening. The beak of the living bird must have been incased in a very heavy horny sheath in order to have possessed the strength necessary in tearing the resistant tissues upon which the species is supposed to have fed.

*Measurements (in millimeters) of skulls of Teratornis in the Los Angeles collection.*

| | No. 13 | No. 244 |
|---|---|---|
| Total length along sagittal line | 213 | |
| Width through postorbital processes | 89.7 | |
| Width of interorbital roof | 52 | |
| Depth through sphenoidal rostrum at orbit | 51.2 | |
| Length of nareal opening | 72.3 | 72 |
| Maximum depth of nareal opening | 36 | 33.2 |
| Depth of beak at anterior end of nareal opening | 41.8 | 39 |
| Depth at middle of nareal opening | 45 | 42.5 |
| Width at anterior end of nareal opening | 36.4 | 35.2 |
| Length of vacuity in palate | 85.8 | 91 |
| Maximum width of this vacuity | 19 | 18 |
| Minimum width of internareal bridge | 11 | 10 |
| Minimum depth of internareal bridge | 4.1 | 3.7 |
| Minimum depth of maxillopalatines | 7.7 | 8.5 |
| Overhang of hook (slightly restored) | 20 | |

*Pectoral arch.*—Since the original description was published, our knowledge of this part of the skeleton has been enlarged by the discovery of the scapula and by the better specimens of the sternal carina. The latter structure is seen to be more developed than was at first thought, though still less than in the Cathartidae. The scapula is essentially cathartine, though less curved and less enlarged at the articular end. The arch is unique in its immense size and in the manubrial and the hyosternal regions of the sternum.

"The sternum shows three points of divergence from the Recent raptorial type. First, its length is greatly reduced until it becomes less than the extreme breadth. Second, the anterior region is expanded until the manubrium becomes a wide, slightly produced mound, excavated at its summit in a gentle, open curve which separates the coracoidal fossae by a distance of 23 mm. Third, the hyosternal processes are developed forward and outward till the anterior and the lateral margins both become strongly concave. * * * The fossa of the pectoralis secundus is relatively small upon the sternum and, as prolonged upon the coracoid, occupies less than half the width of the ventral face of that bone. * * * The anterior margin of the carina is very thick, but this thickness blends backward instead of appearing as a pronounced welt upon the anterior edge of the keel.

"The coracoid and furcula are decidedly cathartid in character. The coracoid shows a wide sternal end tapering to a comparatively narrow shank. The sternal facet occupies less than two-thirds the total width of this end. * * * The hyosternal apophysis is thin and flat, with the sterno-coracoid tubercle but little recurved. On its dorsal aspect the base of the coracoid is comparatively little excavated. Its head region shows striking similarity to *Gymnogyps*. The praecoracoid process is a little less pronounced, thus reducing somewhat the concavity of the axial aspect of the head. The process is pierced by the foramen of the supracoracoid nerve. * * * Considering the great spread of the extremities of the arch, the shaft of the clavicle is much more slender than in any of the Cathartidae; its cross-section is a little more rounded. The

region of the symphysis presents practically the same appearance as in *Cathartes*. The angle of divergence of the two clavicles is very much more open than in any of the true cathardids.''

*Scapula.*—The scapula of *Teratornis* is quite noticeably different from that of the condors proper, it is much straighter in both planes. The distal end is greatly expanded in marked contrast with the Recent birds, while the whole bone is more heavily built. The head is not thrust ventrally to anywhere near the same degree and the whole head region of the bone is distinguished by less positive contours. Just what the significance of these differences may be is not hazarded at this time.

Total length of scapula across the arc, 160 mm.

*Humerus.*—The humerus of *Teratornis* is unique. A large, stout, and rather straight bone of singular contours, if this segment alone were considered, the problem of assignment to its proper systematic position would be extremely difficult. Cathartid characters are almost lost to sight. The deltoid crest, which in the cathartids terminates in a distinct tubercle, is transformed here into a thick, lumpy ridge with almost no tubercle and which actually overhangs the bicipital furrow. The bicipital area on the anterior aspect of the postaxial tuberosity is raised into an immense knob exceeding that found in the pelicans. The bicipital depression thus becomes a deep gorge exceeding that in any Recent form examined by the writer. *Falco*, *Columba*, *Pandion*, and *Diomedea* are all birds with very prominent deltoid crests and of somewhat different habits of flight. In none of these forms is the deltoid crest other than a thin blade of bone and in none of them does the crest extend so far down the shaft. Nor is it clear either what significance the swelling of the postaxial tuberosity may have. A slight approach to the same condition is found in *Falco* and in *Diomedea*, a nearer approach in *Gavia*, *Pelecanus*, and in *Mycteria*, all of which observations go to reduce the value of the character in classification or in determining the habits of the bird. The suggestion has before been made that *Teratornis* was a bird of sailing instead of flapping flight. The only evidence of such habit is the resemblance of sternum to that of *Diomedea*. Study of the humerus contributes in that direction only the suggestion conveyed by the relative straightness of the bone, an evidence measurably counterpoised by the elongation of the deltoid crest.

To make the description serve the greatest number of workers in this field, it is thought wise to compare the humerus with that of *Cathartes aura*.

General form and curvature much the same as in *Cathartes*. The anterior aspect of the proximal region displays two marked differences. The bicipital area is enormously upheaved and the adjacent region strongly excavated. The deltoid crest is likewise thickened and the area of attachment of the pectoralis major becomes a great mound actually overhanging the bicipital furrow. The deltoid crest is long and terminates without a pronounced tubercle. Letting the eye travel down the shaft of the bone to its distal region, one sees the area of the brachialis anticus strongly depressed and with the ulnar portion of the area on an abruptly deeper level than the radial portion. This depression markedly exceeds that in the condors and is about equaled by that in *Cathartes* and in *Gypagus*. There appears nothing distinctive about other parts of the distal region.

The posterior aspect of the proximal end again shows anomalies. There is a superficial resemblance to the gruids in the slightly tumid condition of the area of the internal head of the triceps. The depression about the pneumatic foramen is almost obliterated and the foramen itself is extremely small. The bone is unquestionably pneumatic but certainly it is not so to any unusual degree. The following measurements (in millimeters) of humerus of *Teratornis* are given:

| | |
|---|---|
| Length over all | 329 |
| Length of extremity of deltoid crest | 142 |
| Diameters of smallest part of shaft | 25.4 × 21.4 |
| Diameter through condyles | 62 |

Additional measurements (in millimeters) taken from specimens in the Los Angeles collections are:

| | | | |
|---|---|---|---|
| Length over all | 333 | 315 | 311.5 |
| Transverse diameter of shaft | 26.5 | 25 | 24 |
| Diameter through condyles | 62 | 60 | |

*Ulna.*—The ulna of *Teratornis* is essentially condor-like, the chief difference being that it becomes relatively more slender at the distal end. The bone is 25 per cent longer than in *Sarcorhamphus* and 17 per cent heavier at the proximal end, and yet the carpal ends of the two bones are just equal in size; 22 tubercles mark the attachment of secondaries in *Teratornis* where only 19 are found in *Sarcorhamphus.* The number of tubercles is not only greater, but the distance between adjacent tubercles is also greater by a very appreciable quantity. The feathers of this gigantic bird must then have been developed even in excess of those magnificent quills found in the condors. The following measurements (in millimeters) of the ulna of *Teratornis* are given:

| | |
|---|---|
| Total length | 404 |
| Greatest proximal diameter | 40.3 |
| Greatest distal diameter | 25 |
| Diameters at narrowest point of shaft | 13.3 × 14 |

*Carpometacarpus.*—This bone offers the appearance of a gigantic condor metacarpus except for the same peculiarity noted in case of the ulna—namely, large extremities with slender, elongate shaft. The shafts of the metacarpals narrow to a point even inferior to the condition in *Gymnogyps.* The Recent condors have, as a matter of fact, rather clumsy-looking metacarpals. The only other noticeable points of difference lie in the somewhat more intensified contours of the bone in *Teratornis.* Measurements (in millimeters) of the Carpometacarpus in *Teratornis* follow:

| | |
|---|---|
| Total length | 173 |
| Diameters at narrowest point of metacarpal No. 2 | 13.5 × 9.7 |

*Femur.*—The femur of *Teratornis* is characterized by that same almost columnar straightness that is seen in more distal segments of the limb. In the condors this bone has a pronounced lateral as well as a dorsiventral curvature, so that the proximal portion may project outward at an appreciable angle with the sagittal plane and yet the distal half curve downward to approximate the plane of the tibia. In *Teratornis* this curvature is appreciably less. The result of such straightening is that the distal end of the femur subtends a more pronounced angle with the plane of the tibia; hence the outer condyle of the femur must be more markedly produced in order that the axis of cnemial flexure may be approximately horizontal.

Another feature which contributes to the stocky appearance of the femur is its less positive contours. In the proximal region this tendency is evidenced in the reduction of the trochanter and in the less distinct femoral head. In *Teratornis* the head of the femur can scarcely be said to have a neck at all—a condition sharply in contrast with that in *Gymnogyps* and in *Sarcorhamphus.* Other points of noticeable divergence from the condors are as follows: The pit for attachment of the round ligament is smaller and shallower; the linea aspera is less marked, and the popliteal depression is less profound. In size the bone does not exceed that of *Sarcorhamphus.*

Altogether the characters of the posterior limb of this great bird would suggest that it lacked somewhat of the ambulatory power possessed by the condors.

*Tibia.*—The general appearance of the tibia is positively cathartine, while its proportions might be properly characterized by the word "stubby." Compared even with the condors, which are stout-legged birds, *Teratornis* seems to have been lacking in grace. The length of the tibia is less than that of *Sarcorhamphus* but exceeds that of *Gymnogyps.* The enlargement toward the head begins further down the shaft and is more gradual, and since both tibial crests are less developed the general effect is of thickness and bluntness. It may be recalled that in the ulna and metacarpus slender-

ness with positive contours distinguishes *Teratornis* from the condors; in the case of femur and tibia just the opposite is true. Although these bones are almost incredibly light for a bird of the body-weight *Teratornis* must have had, when taken individually they appear clumsy and thick. The California condor of to-day is a walking bird of considerable power, with long, strong stride which covers considerable distances easily. It seems from study of the leg bones of *Teratornis* that he must have been much less able upon his feet. Such a condition is the more remarkable in view of the difficulty experienced by large birds in taking flight. The Condor often has difficulty in rising from a horizontal surface. What must have been the effort required to launch such a large bulk as *Teratornis!*

*Measurements (in millimeters) of tibiotarsus of Teratornis.*

| | |
|---|---|
| Length from rotular crest to extremity of condyles | 228 |
| Least transverse diameter of shaft | 16 |
| Least sagittal diameter of shaft | 14 |

*Tarsometatarsus.*—In 1910 the new genus and species, *Pleistogyps rex*, was described by the writer from a series of five specimens of the tarsometatarsus. The question of possible specific identity of this tarsus with the skull and pectoral arch described the year before as *Teratornis merriami* was discussed at that time and such identity was considered impossible. The reasons for such conclusions are just as potent to-day as they were six years ago, yet circumstantial evidence must in this case override theory. Hundreds of specimens of *Teratornis* appear in the Asphalt that seem to have no feet. Approximately the same number of tarsi of *Pleistogyps* appear without any body parts. The only possibility is the apparently impossible, and we must credit the incredible. *Pleistogyps* is then announced as a synonym of the prior term *Teratornis.*

Series of the tarsometatarsus bear out the original characterization published for *Pleistogyps rex.*[1]

"Size very large. Intercotylar tuberosity very inconspicuous. Head almost symmetrical upon the shaft. Foot narrow and rotated inward. Inner toe much in rear of outer and reaching almost the same level as middle toe. Groove of middle trochlea not in the sagittal plane."

*Measurements (in millimeters) of the tarsometatarsus of Teratornis.*

| | |
|---|---|
| Total length | 149.6 |
| Greatest transverse diameter of head | 34.5 |
| Greatest sagittal diameter of head | 27 |
| Greatest transverse diameter of foot | 34.6 |
| Greatest transverse diameter of middle trochlea | 13.3 |
| Least transverse diameter of shaft | 15.8 |
| Sagittal diameter of shaft at middle point | 12.3 |
| Width of partition between proximal foramina | 2.9 |
| Transverse diameter of pit into which formina open | 7 |
| Longitudinal diameter of same | 9 |

*Relationships.*—In considering the relationships of *Teratornis* to other raptorial birds one is necessarily restricted to a scrutiny of such characters as may be gleaned from the unassociated skeletal parts—a limitation which is most deplorable since the inter-relationships of the great avian groups are obscure enough even with all the biologic characters of living species available. From a study of such evidence as persists, we may say that, osteologically, *Teratornis* is allied with the cathartiforms. The degree of intimacy of such alliance is, however, not at all easy to estimate. Is the relation of *Teratornis* to the New World vultures more intimate than the relation of the latter group to other raptors? In the discussion of such a question some profit may accrue from an examination of the interrelationships of the various groups of Recent birds of prey.

Beddard[2] assigns all living diurnal raptors to one or another of three great groups of the Accipitres, i. e., the Falconidae, Serpentariidae, or Cathartidae. Under the Fal-

[1] L. H. Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 1, p. 16, 1910.

[2] F. E. Beddard, The structure and classification of birds, London, p. 472, 1898.

conidae he includes all species with the prehensile foot; Serpentariidae is established to accommodate the single South African species, *Serpentarius reptilivorus;* Cathartidae includes only the well-defined group of New World vultures. Beddard admits the aberrant nature of *Pandion* and suggests the possible propriety of establishing for that genus a fourth subdivision of the raptors, although the step is not finally taken.

Practically all authors agree upon the wide hiatus that separates the cathartids from other members of the order Accipitres and a tabulation of the principal differences between the three great groups is given by Beddard as follows:

| | Falconidae. | Serpentariidae. | Cathartidae. |
|---|---|---|---|
| Aftershaft | Present | Present | Absent. |
| Oil gland | Tufted | Tufted | Nude. |
| Muscle formula | A | BXY | (A)XY. |
| Accessory semimembranous | Present | Absent | Absent. |
| Caeca | Rudiments | Rudiments | Absent. |
| Syrinx | Present | Present | Absent. |
| Basipterygoid processes | Absent | Present | Present. |
| Desmognathism | Maxillo-pal | Maxillo-pal | Alinasal. |

A discussion of this table may be properly quoted from its author, as follows:

"It is clear from the few characters—the principal ones, however—given in the above list that the Cathartidae are more aberrant (considering the Falconidae to be the typical birds of prey) than are the Serpentariidae; for the Cathartidae diverge in all eight characters from the Falconidae, while the secretary vulture diverges in only three. What reason is there, it might be asked, to retain the American vultures within this order at all, particularly if the owls are to be (as I think they should be) excluded? The only group which has the distinctive characters of the Cathartidae (besides of course the present group) is that of Herodiones. There only do we find birds with ambiens and expansor secondariorum, without biceps slip, holorhinal, and with rudimentary or absent caeca. The Steganopodes also are not far off. It really comes to the beak and claws, the ceroma, and to the presence of various other structures (*e. g.*, the peculiar palate, the basipterygoid processes) which forbid their association with the Herodiones. The several groups are not far off, but on the whole the American vultures are more like the remaining birds of prey than like the stork tribe."

These remarks suffice to show that the American vultures constitute a class almost by themselves. When studied by the osteologist or the palaeontologist, where perishable characters have been lost this isolation becomes almost perfect. The peculiar type of desmognathism throws the breach with other raptors into higher relief, while the presence of baspiterygoid processes would ally them with a varied assortment of other birds. Study of skeletal parts other than the skull gives no clue to relationships. In very brief, the affinity of cathartiform birds with other raptors is remote and our knowledge of the point of divergence is nil.

In considering the relationships of *Teratornis* to other raptors, the simple statement that the bird is essentially cathartiform would at once narrow the discussion to the degree of kinship with the American vultures only. The first study of the skull of *Teratornis*, when the palatal region was unknown, left the student in doubt as to possible affinities with *Serpentarius*. Since, however, more complete speci-

mens of the skull have been obtained, it becomes clear that the resemblance to *Serpentarius* is a superficial one only.

Beddard's group Cathartidae, which is equivalent to the suborder Sarcorhamphi of the American Ornithologists Union, embraces but 5 genera and a possible 6 species of Recent birds. Osteologically the group is remarkably homogeneous, the differences being a matter of dimensions rather than of other osteologic characters.

*Teratornis*, on the other hand, shows very bold divergence in its osteology from the closely knit family of the Cathartidae, the divergence taking a number of different pathways. The degree of divergence is in excess of those osteologic differences to be noted between most families of living birds classified under one order. It would seem, therefore, incongruous to thrust this aberrant bird into the well-ordered family of the Cathartidae. Upon these grounds it is considered necessary to establish the family Teratornithidae, a family which (so far as our present knowledge goes) contains but a single species.

*Synopsis of characters of Teratornithidae which distinguish it from Cathartidae.*

Elongation and attenuation of the Ulna and metacarpus.
Ruggedness of the humeral head.
Broadening and shortening of the sternum.
Weakness and openness of the furcula.
Relative weakness of the posterior limbs.
Reduction of the trochanter of the femur.
Reduction of the tibial crests.
Columnar character of the tarsometatarsus.
Compression and vaulting of the beak.
Close approximation of the maxillo-palatines.
Lateral and backward extension of the post-auditory prominences.
Reduction of the cerebellar region.
Elliptical form of the foramen magnum.

These differences are marked enough when the parts are under scrutiny and yet except for the characters of the foramen magnum and of the posterior part of the skull, they are recognizable as modifications of structures which are essentially carthartiform. These exceptions are not considered as sufficient wholly to remove the species from the suborder Sarcorhamphi.

## BUTEONIDAE.

### Elanus leucurus (Vieillot).

In the collections at Los Angeles there occurs a single bone, a tarsometatarsus, which represents the kites. The specimen is perfect and corresponds absolutely with the cannon bone from a Recent bird of the same region. Until the last decade, *Elanus leucurus* was fairly common in the open country of southern and middle California. Why its remains are not more abundant in the Asphalt is not easy to say. The very positive suggestion is that the species has had its local rise since Pleistocene time and present conditions show its numbers again declining almost to extinction.

### Circus hudsonius (Linnaeus).

Remains of the marsh hawk are relatively abundant for a small hawk and all the characteristic parts are represented. These remains are of two sizes which probably represent the two sexes although no male of the Recent bird is available for comparison. It is impossible to state what the habits of the Pleistocene marsh hawk were, but at present the species is rather narrowly limited to open and nearly level country. The suggestion conveyed by the fairly abundant remains of *Circus hudsonius* is that the aspect of the Rancho La Brea locality has not greatly changed since Pleistocene time.

#### Accipiter cooperi (Bonaparte) ?.

A hawk of the size and grosser characters of *A. cooperi* is represented by three specimens in the collections at the University. Two of these specimens, representing the tarsometatarsus, are somewhat corroded, so that size and grosser contours alone are discernible. The third specimen is a tibiotarsus which presents no discernible differences from the same segment in the Recent cooper hawk. The tibiotarsus is a less distinctive bone than the cannon bone and the material is so limited in amount that the assignment to species is only tentative.

#### Accipiter velox (Wilson).

This little hawk is represented in the University collections by a tarsometatarsus, tibiotarsus, and coracoid which correspond in size and in osteologic characters with a female specimen of the Recent phase of the species. All specimens are from the same Asphalt lens and the cannon bone and the coracoid were closely associated. It would seem that the species could not have been very abundant in the immediate locality at the time of deposition of the beds.

#### Buteo borealis (Gmelin).

This bird may be properly called common in the Asphalt, although such term is used only in comparison with other small raptors; none of the hawks is common in comparison with the eagles. All parts of the skeleton are represented and the distribution is rather impartial as regards the various lenses. A considerable amount of comparative material of different age and sex has been examined, but no appreciable difference between the Recent and the fossil phases of the species has been discovered. In the same locality to-day this bird is one of the commoner hawks of its type, inhabiting open country where it feeds upon rodents to a large degree. Its occurrence in the Rancho La Brea beds affords no great measure of surprise.

#### Buteo swainsoni Bonaparte.

Characteristic segments of the skeleton of the Swainson hawk occur in both collections examined but they occur with surprising rarity as compared with the species last named. The ecologic position of these two birds is somewhat the same, while the habit displayed by *B. swainsoni*, of going in large flocks in open country and of congregating about waterholes, would seem to expose it to great danger of entrapment by such outpours as must have occurred at Rancho La Brea. There thus seems to be a rather positive suggestion of greater rarity of the species compared with *B. borealis* during the Pleistocene.

#### Buteo sp. (1).

There occur very sparingly among the remains of light-weight buteonids a tarsometatarsus closely resembling that of *Buteo elegans* in its general proportions but at once distinguishable from that species by the weaker trochleae and slightly more slender shaft. It has not been possible thus far to make comparison with the less common *Buteo abbreviatus* or with more southern members of the genus. With some of these living species, the fossil may later be found to coincide.

#### Aquila chrysaëtos (Linnaeus).

Among falconid raptors in general there appears to exist a great range of size variation, owing to the very appreciable discrepancy in the sexes. Large male individuals grade in with small females to form a practically continuous series of great amplitude. For a study of the eagles of Rancho La Brea, the assembling of an extensive series of Recent skeletons for comparison has been out of the question; hence the variability of the Recent phase is not determinable. Scrutiny of all the characters available to the ornithologist seems not to have offered basis for the recognition of geographic races of *Aquila* to-day. Such variation as may be normal for the species

may then be properly looked for in any given locality if a large enough series of individuals be assembled. The almost numberless specimens of Pleistocene *Aquila* from the Asphalt show a considerable range of variation. Whether or not this variation exceeds in amplitude the Recent phase of the species is not possible to state. Certainly the series includes within its limits all Recent *Aquila* material that has been examined and no tangible differences between the two phases are discernible.

### Haliaëtus leucocephalus (Linnaeus).

This species has been commented upon at some length in an earlier paper[1] on the eagles of Rancho La Brea, and at a previous point in the present paper under the caption of "general problems." Attention was there called to the fact that *Haliaëtus leucocephalus* occurs in the Asphalt beds in a highly variable phase as compared with the recent birds from any one faunal area. This variability includes the two Recent races of the species, hence we seem to have the pleasurable experience of placing the finger upon the point of divergence of two of the smallest phylogenetic twigs, the geographic race. The series of material has been greatly enlarged by later excavation; nevertheless the number of specimens representing this species is surprisingly small in comparison with *Aquila*. All characteristic parts of the skeleton are represented in the collections.

### Morphnus woodwardi Miller.

*Morphnus woodwardi* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 12, p. 312, 1911.

To the type specimen of this species, which for some time remained unique in the University collections, there have now been added several specimens of the tarsometatarsus. These additional specimens are found in the collections at the University and at Los Angeles. The material thus added is not extensive, but it is sufficient to enlarge our understanding of the species to this extent—that the type specimen may be considered to be in all probability from a small female bird. Specimens quite appreciably smaller and others larger than the type have been examined.

As yet no success has attended efforts to differentiate other parts of the skeleton from the great mass of unassorted eagle bones. With six species of eagles and one vulturid of eagle-like proportions commingled indiscriminately, the completion of that task seems somewhat remotely distant.

Diagnostic characters of the tarsometatarsus are quoted from the original as follows: "Resembling *Aquila* in general, but 30 per cent longer; shaft narrower, ligamentous bridge shorter, anterior proximal depression shallower and less defined; papilla of tibialis anticus placed much higher on the shaft; ridges of the hypotarsus less produced; foot narrower and trochleae smaller."

The collections at Los Angeles contain a series of specimens of the tarsometatarsus of *M. woodwardi* almost perfectly preserved. There is evident a considerable range of variation in dimensions, but the series is a continuous one. Length is taken from the intercotylar prominence through the middle trochlea. The shaft is measured transversely at its narrowest point.

*Measurements (in millimeters) of tarsometatarsus of Morphus woodwardi.*

| No. | Length. | Head. | Foot. | Shaft. | No. | Length. | Head. | Foot. | Shaft. |
|---|---|---|---|---|---|---|---|---|---|
| 1...... | 138 | 24 | ........ | 11.7 | 5..... | 130 | 23 | 25 | 11 |
| 2...... | 136.5 | ........ | 28.7 | 12 | 6..... | 126 | 22.3 | ........ | 10.5 |
| 3...... | 135.5 | 25 | 27.5 | 12 | 7..... | 132.5 | 22 | 26 | 9.6 |
| 4...... | 135 | 22.8 | ........ | 10.8 | 8..... | 134 | 23 | 26 | 9.7 |

[1] L. H. Miller. Univ. Calif. Publ. Bul. Dept. Geol., vol. 6, No. 12, pp. 305–316, 1911.

### Morphnus daggetti Miller.

(See Plate 9.)

*Morphnus daggetti* Miller, The Condor, vol, 17, pp. 179–181, 1915.

This remarkable bird is now known from two perfect tarsometatarsi, two fragments of the same segment, and an almost complete tibiotarsus. All specimens with the exception of one fragment in the University collections are from the Los Angeles Museum and were taken from the same lens, pit No. 4, by that institution. The tarsometatarsus was briefly characterized in comparison with the more typical eagles as follows:

"Assignment of this species to the genus *Morphnus* instead of to the genus *Geranoaëtus* is based upon differences in the head of the tarsometatarsus. The length of the tendinous bridge is less in *Morphnus*, as is likewise the development of the outer hypotarsal ridge. The difference is constant though slight. The affinities of the fossil specimen as indicated by these characters are with *Morphnus*.

"Distinctive characters of the species are: extreme elongation of the tarsal shaft; weakness of the distal trochelae, which are set less obliquely upon the shaft and are less deeply grooved than in *Aquila;* extreme reduction of the ratio of power arm to resistance arm. In *Aquila* this last-named ratio is 0.303, in the species under discussion it is but 0.125."

*Measurements (in millimeters) of tarsometatarsus of M. daggetti.*

| | |
|---|---|
| Length over all | 167 |
| Transverse diameter of head | 20.8 |
| Transverse diameter of foot | 22.8 |
| Transverse diameter of shaft at narrowest point | 9.1 |
| Length of power arm | 20.6 |
| Ratio of power arm to weight arm | 0.125 |

Since the species was first announced there has been found in the same section of the excavations with one of the proximal shank fragments, a specimen of the tibia which articulates perfectly with it. The specimen is in excellent condition except that the head of the bone above the peronial crest has been lost. Even the most conservative restoration of the missing part would show the same striking elongation as is displayed by the tarsometatarsus. Such restoration would indicate a total length of 215 mm., whereas the corresponding bone of the same diameter from *Haliaëtus* measures but 157 mm. In the fossil specimen, the distal end of the fibular rudiment is not traceable so far down the shaft of the tibia as it is in *Haliaëtus*, the intercondylar depression on the anterior and distal surfaces is shallower, while the whole bone gives the effect of being straightened, especially when seen from the rear. The general nature of the bone harmonizes well with the impression given by the tarsometatarsus—that of an ambulatory habit and probably a complete sacrifice of the prehensile power of the foot. The case seems quite comparable in this respect with that of *Polyborus* except that the bird is truly an eagle, while *Polyborus* is osteologically distinct from any of the raptorial groups with which the writer is acquainted.

### Geranoaëtus grinnelli Miller.

*Geranoaëtus grinnelli* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 12, p. 314, 1911.

This species, like the next, has been found repeatedly in the collections examined. The two forms have thus far been recognizable only from the tarsometatarsus and differences noted in the original descriptions hold quite constantly true.

"In its tarsometatarsus *Geranoaëtus grinnelli* resembles *G. melanoleucus*, but it is more robust and shows superior strength by greater production of the hypotarsal ridge and lower position of the papilla of the tibialis anticus. Details of comparison are as follows:

"Anterior view. The proximal depression is not so deep; the proximal foramina are very close together and almost on the same level; and the outer attachment of the

tendinous bridge is in the form of a rounded papilla instead of an elongate ridge. The head of the bone at the extreme summit is just equal in width to that of *G. melanoleucus*, but narrows less rapidly as it merges into the shaft. The papilla of the tibialis anticus is farther down the shaft, thus giving a ratio of power arm to weight arm of 23.8 per cent as against 18.4 per cent in the Recent bird. * * *

"Posterior aspect: The most striking differences noted from this aspect are the closer approximation of the hypotarsal ridges and the prolongation of the inner ridge to a greater distance down the shaft. * * *

"Proximal articular surface: From this viewpoint the fossil presents three points of divergence from the Recent species. The anterior and the external borders are both indented instead of being nearly straight. The external facet thus assumes a more rounded outline. The hypotarsal ridges are produced to a greater degree and, although the space included between them is narrower, the inner ridge seems less deflected toward the median line. A cross-section of the hypotarsal groove thus presents a quite different outline."

The following are the dimensions in millimeters, of the type specimen, tarsometatarsus: Length over all, 109; length to middle of papilla of tibialis anticus, 26; transverse diameter of head, 20; transverse diameter of foot, 22.5; least transverse diameter of shaft, 10; greatest sagittal diameter of head, 17.3.

### Geranoaetus fragilis Miller.

*Geranoaëtus fragilis* Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, No. 12, p. 315, 1911

Though fairly common in the Asphalt, this species, like the last mentioned, is still recognizable only by the tarsometatarsus, originally described as follows:

"Length equal to *G. melanoleucus* but width much less; papilla of the tibialis anticus much higher on the shaft; proximal depression and proximal foramina much the same. Anteroexternal ridge of the shaft sharper; inner hypotarsal ridge placed much nearer the center of the shaft; hypotarsal ridges placed much nearer together; and the intervening furrow more than a semicircle in cross-section.

"In size the closest approach is to *Geranoaëtus grinnelli*. It is, however, distinguishable by its greater slenderness, the higher position of the papilla of the tibialis anticus, the greater distance between the proximal foramina, the shorter supratendinal bridge, and the elongation of the papilla at the inner end of this bridge to form a vertical crest which merges upward into the margin of the proximal articular surface. On the posterior side the inner hypotarsal ridge is not prolonged down the shaft, but is stopped abruptly by the posterior opening of the inner proximal foramen. This foramen in all specimens examined opens posteriorly at the exact lower limit of the inner hypotarsal ridge, whereas in all specimens of *G. grinnelli* examined, the base of this ridge extends down the shaft beyond the foramen and upon its inner side.

"* * * The transverse diameter of the head and of the foot of the bone just equal the corresponding dimensions of *Archibuteo ferrugineus*, while the length exceeds that in *Aquila*. The ratio of power arm to weight arm in flexure of the tarsal joint is 16.6 per cent, a ratio just equal to that in *Morphnus woodwardi* and far inferior to that in *Geranoaëtus grinnelli*."

The following are the measurements (in millimeters) of the type specimen, Tarsometatarsus: Length over all, 112.6; length to center of papilla of tibialis anticus, 18.6; transverse diameter of head, 18; transverse diameter of foot, 19.4; least transverse diameter of shaft, 8.1; sagittal diameter of head, 14.8.

## FALCONIDAE.

### Falco mexicanus Schlegel.

This species is more abundantly represented in the Asphalt beds than any other of the family of true falcons. In both the University collection and in that at the Los Angeles Museum there are to be seen the characteristic bones of the skeleton, such as

the humerus, the posterior limb bones, and the coracoid. These specimens correspond perfectly with the same segments of the Recent skeletons at hand. The remains of a specimen recently entrapped in waste oil flows proves the susceptibility of the bird to the attractions of the trap. The locality at present offers just such environment as seems to please this bird of the open country.

### Falco columbarius Linnaeus.

This species is represented by at least two specimens in the University collections, one a tarsometatarsus and one a tibiotarsus. The specimens, in a perfect state of preservation, were taken from the same excavation, though at different times. A slight discrepancy in size indicates that different individuals are represented. Comparison is made with a single specimen of *Falco columbarius suckleyi* in the California Museum of Vertebrate Zoology. The Recent specimen is very slightly larger than the fossil material but the difference is not significant and the proportion of parts in both segments remains constant. There seems no reason why the fossil should not be referred to the same species as the Recent bird if we waive the ever-present question in such cases where osteological characters alone persist.

### Falco sparverius Linnaeus.

This untamed pigmy among raptors is well represented in the various asphalt lenses, though nowhere common. Characteristic bones, such as the Tibiotarsus, tarsometatarsus, and humerus occur in both the larger collections examined. The habits of the Recent bird are so widely diverse as to contribute nothing to our impression of the Pleistocene landscape.

### Falco, sp.

In the University collections, two specimens of the tibiotarsus appear, which represent a falcon of a size intermediate between the larger *F. mexicanus* on the one hand and the smaller *F. columbarius* on the other. Proper reference of the species is not possible in the absence of comparative material from Central and South America. Certainly none of the species at present known to California will accommodate these specimens.

The medium-sized *Falco fusco-cerulescens* of South and Central America, which reaches the Mexican boundary in Arizona and New Mexico, and *Falco aurantius* of slightly more restricted northward diffusion correspond very closely in size with the fossil material. Taking the recorded measurements of the Recent birds, we find the average size ratio of *F. columbarius* to *F. fusco-cerulescens* to be 77 per cent. Comparing the fossil *Falco* material with the corresponding bones of *F. columbarius* we obtain a ratio of 75 per cent. This means little beyond the fact that the finger of probability is pointed to the southward as the home of the nearest living relative of the undetermined *Falco*.

The collection at Los Angeles contains a perfect right tarsometatarsus of an adult bird which may properly be referred to the same species. The dimensions of the tarsometatarsus are as follows (in millimeters): Length, 47.5; head diameter, 10.9; foot diameter, 11.4; shaft diameter, 4.6.

### Polyborus cheriway (Jacquin).

This representative of a degenerate raptorial group, so distinctive in its habits and in its osteologic characters, constitutes one of the very interesting aspects of the Rancho La Brea fauna. It is the most abundant of the small raptors, though closely rivaled by *Neophrontops* in point of numbers. The ambulatory habit and the necrophilous appetite would render the bird particularly liable to entrapment in the asphalt outpours, hence the only element of surprise hinges upon its geographic distribution. All Recent members of the subfamily Polyborinae are at present limited to habitats more tropical than the Los Angeles region. Not even as a straggler has any Recent poly-

borine been recorded from the coast of California, yet *Polyborus* was plainly quite an abundant bird during the Pleistocene.

Assignment of the fossil remains of *Polyborus* to the species, *tharus*, was published in a tabulation of west American Pleistocene avifaunas.[1] Conclusions were based upon comparison with a single specimen of *Polyborus* from Argentina, designated *P. tharus*. The fossil remains correspond perfectly in osteologic characters and in proportion of one segment to another with this specimen of *P. tharus*. The size of the fossil is very slightly less than that of the single specimen from South America.

Within the last few weeks the California Museum of Vertebrate Zoology has placed in my hands the distal segments of the posterior limb of a large specimen of *Polyborus cheriway* from Salvador. The ratio of tibiotarsus to tarsometatarsus is identical with that in *P. tharus* and the specimen of *P. cheriway* is slightly the larger bird. Ridgway,[2] in his monograph on Polybori, places the maximum of *P. cheriway* about equal to the minimum of *P. tharus* in length of the tarsus. It is assumed that the Recent specimen of *P. cheriway*, then, is of maximum size while that of *P. tharus* is near the minimum for that species.

Ridgway's measurements are of museum skins and fall slightly short of the dimension as taken from the cleaned bone, but the ratio of his maximum to minimum should remain the same and furnish a basis for calculating (from the disarticulated specimens) the average size of each species when measured by the osteologist. For *Polyborus tharus* such a series of calculations yields an average length of tarsometatarsus far above that of the fossil species, while the latter is almost identical with the calculated average of *P. cheriway*. It would seem more proper, therefore, to assign the Rancho La Brea caracara to the Mexican species *Polyborus cheriway* than to the Argentine *P. tharus*, although as between the two Recent specimens at hand the size corresponds most closely with the South American bird.

The zoogeographic interest in the question is no less positive, however, with this change of assignment of the fossil remains. Assuming the species to be *P. tharus*, the advance of glacial cold from the north might have driven the bird across the equatorial zone to a south temperate zone, whence its return later would be barred by the equatorial forest area. Such interpretation of facts would have no bearing on the question of post-glacial amelioration of climate in the northern hemisphere. On the other hand, if we consider the Rancho La Brea *Polyborus* to belong to the Mexican species *cheriway*, the case is different. The present habitat of *Polyborus cheriway* is very abundantly stocked with individuals offering no evidence of decadence. The area inhabited widens out toward the north. There is no appreciable physiographic barrier to diffusion in that direction except it be the barrier of climate. The very positive suggestion therefore is that post-glacial advance of isothermal lines has not reached that degree attained at the time of formation of the Rancho La Brea asphalt deposits.

The table gives measurements (in millimeters) of the tarsometarsus of *Polyborus* from the Los Angeles collection.

| Length. | Head. | Foot. |
|---|---|---|
| 93 | 13.4 | 14.5 |
| 89.7 | 13.3 | 14.5 |
| 86.2 | 13.5 | ........ |
| 86.3 | 13.4 | 14 |
| 92.4 | 13 | 14.7 |
| 89.6 | 14 | 15 |
| 90 | 13 | 15 |
| 87.8 | 13 | 14.6 |
| 87 | ........ | 13 |
| 85.5 | 14 | 15 |
| 83 | 13.8 | 14.3 |
| 94 | 13 | 15.5 |
| 88 | 13.2 | 14.8 |
| 87.6 | 13 | 14 |

An additional series of 32 specimens was examined from another part of the Los Angeles collection. In all the parts assembled there is noticeable a peculiar tendency to robustness of the shorter specimens. The series shows a perfect intergradation in length between 83 and 94 mm., yet all the shorter specimens display a stockiness of

[1] Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, No. 5, p. 112, 1912.

[2] R. Ridgway, Bull. U. S. C. and G. Surv. of Terr., vol. 1, No. 6, p. 451, 1876.

form. The character alone is scarcely sufficient to prove the presence of two species, yet the suggestion is a very positive one. The following measurements of the femur and tibia are in millimeters:

| Femur: | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Head through inner condyle..... | 65 | 70 | 65 | 71 | 69.4 | 70 | 68.6 | 70 | 67.6 |
| Transverse shaft diameter....... | 7.9 | 7.4 | 7.2 | 7.7 | 7.6 | 7.6 | 7.7 | 8.3 | 7.9 |

| Tibia: | | | | |
|---|---|---|---|---|
| Length from peronial condyle to intercondylar notch.............. | 110 | 107 | 106 | 105 |
| Diameter through condyles.......................................... | | 13 | 12 | 13 |

## VULTURIDAE.

### Neophrontops americanus Miller.

(See Plate 8, Figs. 4–5.)

*Neophrontops americanus*, Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 9, No. 9, p. 105, 1916.

This species has so recently been described and commented upon in the above paper that no additional light has yet been thrown upon the subject. Brief description of the type and cotypes and repetition of the text-figures are here quoted for the convenience of the worker.

*Tarsometatarsus.*—"The type specimen is a perfect specimen as well preserved as though freshly macerated from the flesh. The degree of ossification and the distinctness of the intermuscular lines indicate an individual of advanced age. Other members of the series have smoother contours. The specimen of *Neophron ginginianus* available for comparison appears from characters of the bone surface, to be a slightly sub-adult bird. In general proportions the two bones are almost identical, the ratio of shaft diameter to length being 0.072 in *Neophrontops* and 0.077 in *Neophron.* When viewed from in front, the Asphalt specimen is seen to have less pronounced excavation about the papilla of the tibialis anticus; that papilla is thus more prominent and is placed higher on the shaft. * * * Distally the shaft widens more gradually into the foot and the trochleae are narrower and weaker. They are also more nearly on the same level.

"In the hypotarsal region, *Neophrontops* is seen to have the hypotarsal ridges more prominent, closer together, and without an incipient third ridge between. The hypotarsus is set off more abruptly from the shaft below; the bone is more excavated so that parts of the proximal end are appreciably thinner than in *Neophron.* The plantar tendons occupy a deeper groove along the posterior face of the shaft."

*Tibiotarsus.*—"The tibiotarsus of the Asphalt species is almost absolutely identical with that of

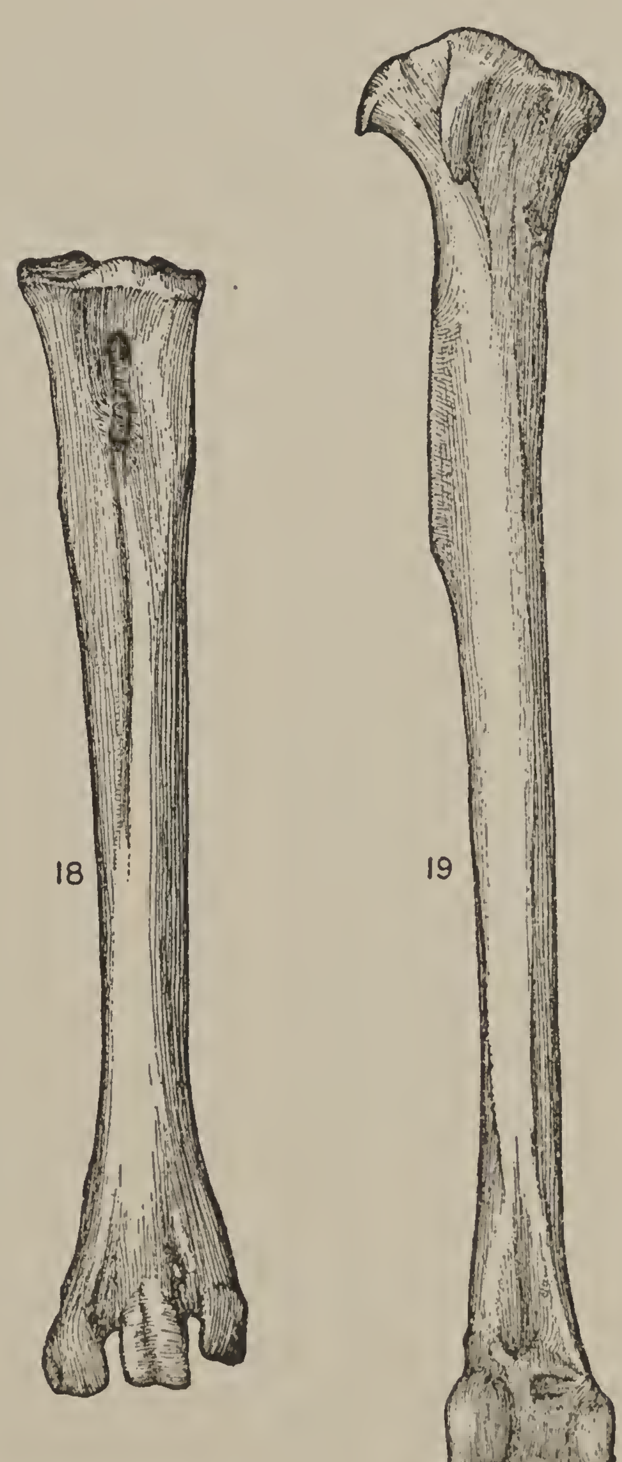


Fig. 18.—*Neophrontops americanus.* Tarsometatarsus. Natural size.
Fig. 19.—Same. Tibiotarsus. Natural size.

*Neophron*, except that the shaft is slightly more slender and the cnemial crest more prominent. The tunnel under the osseous supratendinal bridge is similarly small and quite in keeping with the weakness of the flexor tendons. The furrow leading to this tunnel is almost obsolete, more nearly so even than in the American *Cathartes*. The intercotylar depression is practically identical with that of *Neophron*. On the inner face of the inner condyle occurs a rugosity marking the attachment of articular ligaments. This rugosity is raised to a tubercle in active raptors, is less in *Neophron*, and is least in *Neophrontops*. Seen from the proximal end, the two bones show an identical pattern. From the rear the same holds true."

*Humerus*.—"This bone in the fossil species is practically identical with that of the Recent *Neophron*. Size, curvature, condyles, and muscle scars are almost as nearly alike as though taken from the same individual. Certainly no tangible difference is noticeable to the writer."

### Neogyps errans Miller.

*Neogyps errans*, Miller, Univ. Calif. Publ. Bull. Dept. Geol., vol. 9, No. 9, p. 108, 1916.

This species was published upon with the one immediately preceding, and like the latter has received no additional light further than the repeated confirmations of conclusions reached earlier in these studies.

*Tarsometatarsus*.—"Slightly smaller than the minimum of *Aquila chrysaëtos*, but general proportions much the same as in that species. The contours much less rugged; papilla of the tibialis anticus more rounded and knob-like and placed higher upon the shaft; distal trochleae and outer ridge of the hypotarsus weaker than in *Aquila* * * * "

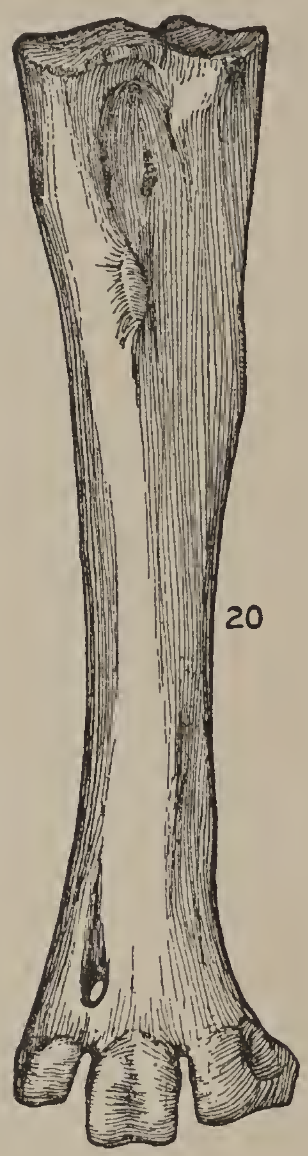


Fig. 20.—*Neogyps errans*. Tarsometatarsus. Natural size.

"The general impression made by the tarsometatarsus is of a stockily built bird with a general resemblance to *Gypaëtus*, though less in size than *Gypaëtus barbatus*. With the exception of the immediate region of the anterior openings of the proximal foramina, the contours of the bone are less rugged than in *Gypaëtus;* the antero-external angle of the shaft is less sharp; the trochleae are less distinctly set off from the shaft and are less deeply grooved; the outer hypotarsal ridge is less developed. All these are characters which in general distinguish the vulturids from the more predaceous raptors and are evidences of degeneracy wherein *Neogyps* seems to have exceeded *Gypaëtus barbatus*.

*Measurements (in millimeters) of a series of 14 specimens of the tarsometatarsus of Neogyps errans.*

| | Type. | Average. |
|---|---|---|
| Length, intercotylar to extreme convexity of middle trochlea.... | 88.0 | 87.8 |
| Transverse diameter of head.................................. | 19.6 | 19.6 |
| Transverse diameter through trochleae........................ | 22.6 | 22.4 |

## STRIGES.

The nocturnal raptors have been made the special subject of a recently published report by the present writer,[1] This memoir, therefore, has little to add to our knowledge of the group as represented at Rancho La Brea, Among the introductory remarks in that bulletin the following points were brought out:

1. As compared with diurnal raptors, owl remains are rare both in point of numbers and of species.
2. This discrepancy is out of harmony with the balance of fauna as between nocturnal and diurnal raptors to-day.
3. Owls were possibly less attracted to the Asphalt trap than were hawks, although in Recent outpours owls are among the most commonly entrapped forms.
4. More copious outpour during the Pleistocene may have resulted in rapid entombment of small forms, leaving only the larger victims exposed to view.
5. Results of this more rapid entombment would be that the small hawks and the owls would find bait less constantly before them.
6. Cooling of the Asphalt surface at night may have rendered the trap less dangerous to owls than to birds hunting by day.

Six species are recorded in the above discussion and the conclusions regarding their relative abundance have been borne out by the continued studies since. One species, *Glaucidium gnoma*, has been added to the list on the basis of a single bone.

### Aluco pratincola (Bonaparte).

The remains of the barn owl occur in all the lenses and at various depths, making this bird by far the most abundant of the Strigine species noted in these beds. Careful study of the remains fails to show any tangible diversion from the Recent phase of the species. *Aluco* is a hunter of rodents, particularly of gophers of the genus *Thomomys*. According to Dr. H. C. Bryant, of the California Fish and Game Commission, these rodents perform considerable journeys above ground at night and have been entrapped in considerable numbers by crude oil spread upon the surface of roadways. The open country of the Rancho La Brea region would constitute excellent hunting-ground for a nocturnal bird with a special taste for these rodents. Herein lies, perhaps, the reason for the abundance of *Aluco* in comparison with other owl remains. The surprising fact is that both the owl and its customary prey are not more common than they are in these beds.

### Otus asio (Linnaeus).

The screech owl is known from a single specimen of the tarsometatarsus in the collections at Berkeley. This bone is identical in character with the Recent *Otus asio bendirei* of California.

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[1] Univ. Calif. Publ., Bull. Dept. Geol., vol. 9, No. 8, p. 97, 1916.

### Bubo virginianus (Gmelin).

The results of a very careful study of *Bubo* remains published in the bulletin on owls include the following points:

1. The Pleistocene horned owl displays a greater range of variation than does any of its Recent races in a given locality.
2. An extended series of the remains is necessary to establish specific homogeneity.
3. As in *Haliaëtus leucocephalus*, the Pleistocene phase of the species includes within its limits of variation a northern large race and a southern small race of Recent birds.

### Asio wilsonianus (Lesson).

### Asio flammeus (Pontoppidan).

Studies of the Recent remains of these two species reveal the fact that *A. wilsonianus* is differentiated from *A. flammeus* by possession of a shorter, stouter tarsus but a longer tibia. These differences in proportion represent the only noticeable differences as regards the limb bones.

In a collection of unassorted parts representing both birds, it would be extremely difficult to separate the one species from the other on account of variations with sex and with age. Further study of the Rancho La Brea collections goes to support the impression announced in earlier papers—*i.e.*, that both species of *Asio* are represented, yet a question must be conceded. In view of the great variability of the Pleistocene phases of other birds, such as *Bubo*, *Haliaëtus*, etc., it can not be denied that the *Asio* remains from the Asphalt possibly represent a single species of greater variability than either *A. wilsonianus* or *A. flammeus*.

The abundance of *Asio* in the Asphalt collections is about equal to that of *Bubo*.

### Speotyto cunicularia (Molina).

The rarity of *Speotyto* remains is quite out of keeping with the comparative abundance of the bird to-day. This discrepancy may in part be due to the fact that insects constitute a very large factor in its dietary. Tiny Recent lenses, 12 to 15 inches in diameter, contain tangled masses of its bones. In such small outpours, insect bait would be effective, especially as this little owl hunts extensively by day.

Remains of the species are less abundant in the Pleistocene matrix than are those of *Asio*.

### Glaucidium gnoma Wagler.

A single perfect specimen, the tibiotarsus, represents the pigmy owl in the Asphalt collections. The specimen was taken from pit No. 4 of the Los Angeles Museum excavations at a depth of 9.5 feet. Compared with the corresponding segment of a male bird from Los Angeles County, it is seen to be of slightly greater size, but otherwise indistinguishable. In southern California the Recent species is a bird of the mountains rather than of low country; hence even its rare occurrence in the Asphalt is a matter for some surprise.

### Geococcyx near californianus.

In both the larger collections examined the characteristic limb bones of a neomorphine bird quite consistently larger than the Recent *Geococcyx californianus* occur sparingly. The tarsometatarsus, tibiotarsus, and the humerus are known. These

bones are appreciably longer and the humerus is more robust than in the Recent species. Access to skeletons of the South American neomorphs has not been afforded the writer; hence a more positive expression regarding the Rancho La Brea bird is not made.

### Colaptes cafer (Gmelin).

The peculiar ground-foraging habit of the flicker seems to have prevailed also in the Pleistocene and to have led to his occasional entrapment in the Asphalt—the sole representative of his guild in these beds. Such characteristic bones as the tarsometatarsus and the ulna are found in the two larger collections studied.

## PASSERES.

A considerable number of passerine remains have been examined from both collections studied. The smaller species of the order are commonly found in secondary pockets of the greater lenses, thus suggesting that they were entrapped in marginal areas of the greater outpours. An alternative suggestion is that small areas of very soft asphalt remained about the mouths of vents that produced the larger masses. After the greater portion of the surface had become sufficiently dried or dusted over to support the weight of such small creatures without entangling them, this fresh material in the immediate neighborhood of the outpour would prove their undoing. The remains of beetles occurring in such pockets adds to the strength of the latter hypothesis. The remains of larger passerines, of the genus *Corvus*, are not thus confined to small pockets but occur in the same fashion as do the small hawks and vultures.

In a discussion of the passerine bird remains from the Asphalt, the present writer is obliged to confess a lack of confidence in his ability to distinguish between the small passerine species by inspection of single, unassociated parts of the skeleton. The humerus of a small icterine such as *Euphagus* presents no great differences from that of *Agelaeus*, a bird of the same family but of different habits. Only where the entire skeleton of an individual can be studied should there be hazarded a conclusion as to its identity. Species and even genera of Recent passerines are distinguished by characters not to the least degree reflected in the skeleton. Such species or genera may to-day have entirely different habits and distribution, hence an error in assignment of the Pleistocene specimen to a group of Recent birds would perhaps lead to grave error in the interpretation of results.

There are to-day about the vicinity of the asphalt beds such passerines as *Agelaeus*, *Sturnella*, and *Otocoris* and there occur in the asphalt lenses, the remains of passerines indistinguishable from these birds. In all probability the genera are the same but there is lacking the assurance that would warrant positive statement of such identity. In the few instances recorded below the quantity and character of the material seems sufficient to justify publication of conclusions.

### Corvus corax Linnaeus.

The raven occurs as by far the most abundant passerine in the collections. Practically all parts of the skeleton are preserved including cranium and rostrum. All coincide perfectly with the corresponding parts of the Recent local species *Corvus corax sinuatus*. It is not at all surprising to find this omnivorous plainsman quite commonly represented in both large collections.

### Corvus brachyrhynchos Brehm.

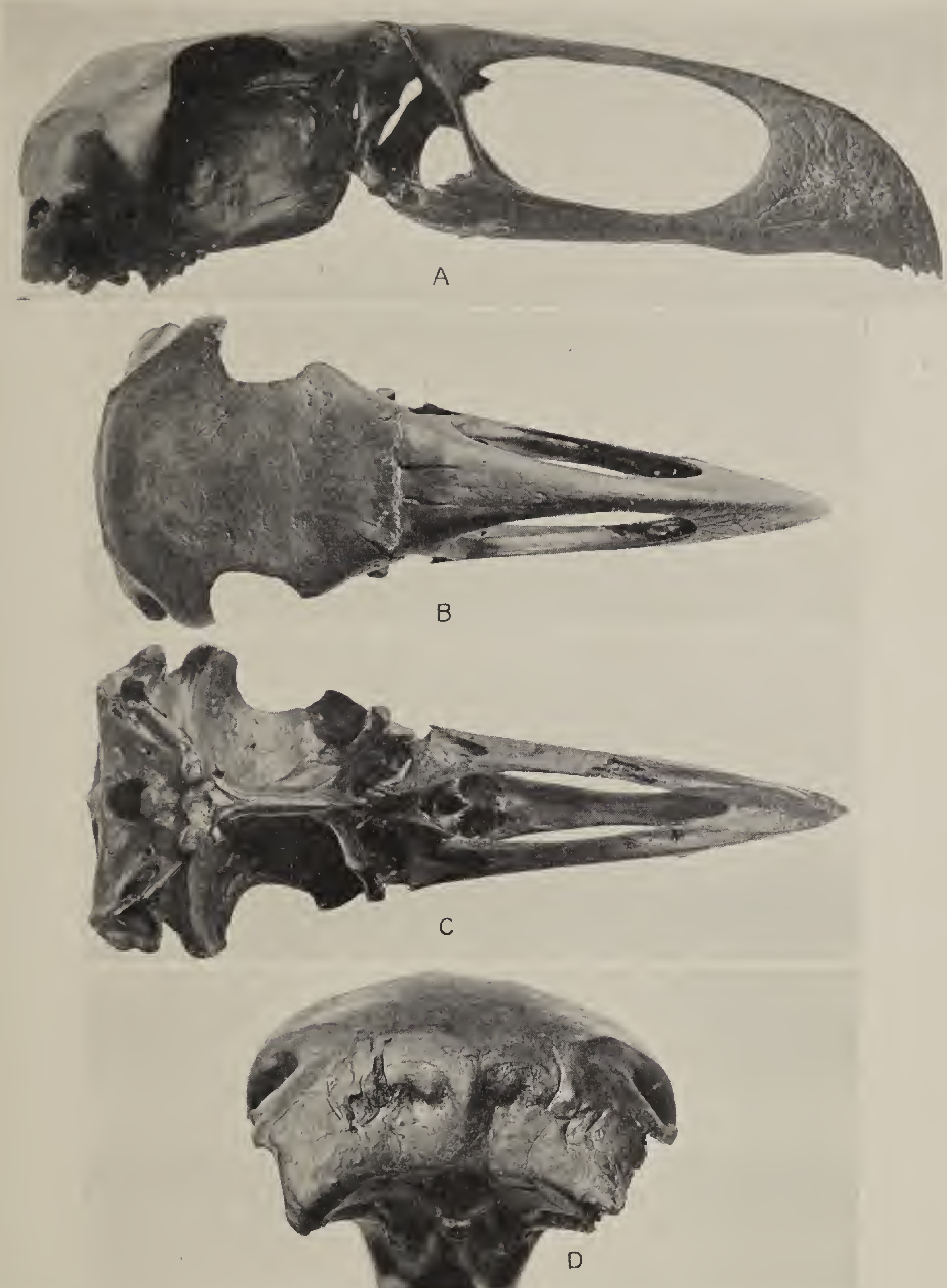
The crow is much less abundant than the raven in the Asphalt but still its remains are found fairly well distributed through the lenses.

### Sturnella neglecta Audubon (?).

The remains of a bird indistinguishable from the meadow lark occur so consistently and the various skeletal parts check so completely with those of the Recent bird that little doubt remains in the mind of the writer as to the identity of the fossil with the Recent species.

### Lanius ludovicianus Linnaeus.

The shrike is represented by a complete skull with its so characteristic beak and nareal region that assignment of the fossil specimen is made with some degree of assurance.




*Teratornis merriami.* Skull. A, from right side (× 5/9 approximately); B, from above (× 1/2 approximately); C, from below (× 1/2 approximately); D, from rear (× 3/4 approximately). Specimen in Los Angeles Museum.


*Teratornis merriami.* A, furcula anterior view (× 3/8, approximately); B, furcula lateral view (× 3/8, approximately); C, coracoid, dorsal view (× 3/8, approximately); D, sternum, dorsal view (× 3/8, approximately); E, sternum, left lateral view (× 2/3 approximately). Specimens in Los Angeles Museum.


*Teratornis merriami.* A, sternum, anterior view (× ½, approximately); B, pelvis, dorsal view (× ⅔, approximately); C, humerus, anterior view (× ½, approximately); D, humerus, posterior view (× ½, approximately); E, humerus, end view of head (× ½, approximately); F, humerus posterior view (× ¼, approximately). Specimens in Los Angeles Museum.


*Teratornis merriami.* A, carpometacarpus, dorsal view (× ½, approximately); B, phalangeal, dorsal view (× ½, approximately); C, femur, posterior view (× ⅖, approximately); D, femur, anterior view (× ⅖, approximately); E, tibiotorsus, anterior view (× ⅖, approximately) F, tibiotorsus, external view (× ⅖, approximately); G, tarsometatarsus, anterior view (× ½, approximately); H, tarsometatarsus, posterior view (× ½, approximately). From specimens in Los Angeles Museum.


*Cathartornis gracilis*—A, B, skull (× $\frac{1}{2}$, approximately); C, carpometacarpus (× $\frac{6}{10}$, approximately).
*Neophrontops americanus*—D, E, rostrum (1/1, approximately).
*Morphnus daggetti*—F, tibiotarsus (× $\frac{2}{5}$ approximately); G, H, tarsometatarsus (× $\frac{6}{10}$, approximately). From specimens in Los Angeles Museum.


*Parapavo californicus*, tarsometatarsus; A, from front; B, from axial side; C, from proximal end; D, from distal end. Approximately natural size.

VI.

# AVIAN REMAINS FROM THE MIOCENE OF LOMPOC, CALIFORNIA.

By LOYE MILLER.

With nine plates and one text-figure.

## CONTENTS.

# AVIAN REMAINS FROM THE MIOCENE OF LOMPOC, CALIFORNIA.

By Loye Miller.

## INTRODUCTION.

The material which forms the basis of the present study was encountered by Dr. David Starr Jordan during his studies of the fossil fishes of the Lompoc diatomaceous shales. Through the courtesy of Dr. Jordan and of Mr. Edward J. Porteous, of Lompoc, the bird remains were referred to the present writer for determination and the type specimens were most generously deposited in the Museum of Palaeontology at the University of California.

The collection comprises a total of some ten specimens representing more or less completely articulated skeletons or part skeletons of birds that had been entombed in various sprawling attitudes within a matrix of almost pure diatomaceous ooze, here accumulated in beautifully laminated beds of great thickness. As the rock is taken out for commercial purposes, it cleaves along the old bedding planes and reveals the carbonized bone in sharp contrast against the almost pure white background of the matrix. This carbonized material is extremely friable and is easily dusted out with a pledget of cotton upon a tooth pick, leaving a fairly perfect imprint of one aspect of the bone. Pressure has distorted the form but little, mainly resulting in a flattening of the bone shafts. Excellent glue casts of these imprints were taken by Mr. J. W. Lytle. The slabs were double photographed by Mr. L. E. Wyman, resulting in reversal of shade and the effect of relief instead of depression. These photographs were in turn worked over by hand under the lens by Mr. J. L. Ridgway. The personal interest taken by these gentlemen is greatly appreciated by the author. Generous financial assistance was rendered by the Carnegie Institution of Washington.

## NATURE OF THE DEPOSIT.

Jordan and Gilbert,[1] in a paper entitled "The Fossil Fishes of Diatom Beds of Lompoc, California," give an interesting account of this unique deposit. Certainly the magnitude and the purity of the accumulation of diatom shells is most astonishing. Some square miles of the material, laid down to a maximum depth of 1,400 feet,

[1] David Starr Jordan and J. Z. Gilbert, Leland Stanford Jr. Univ. Publ., Univ. Ser., Feb. 1920.

lie exposed in the vicinity of the town, where it is the basis of an industry employing from 2,000 to 4,000 men in its removal.

Regarding the diatomaceous matrix in which the vertebrate remains have been discovered, Jordan and Gilbert quote a letter from Dr. Albert Mann, of the Carnegie Institution of Washington, as follows:

1. Marine with no infiltration of fresh or of brackish water forms.
2. Not plankton material. Diatoms all large and massive. Heavy sponge spicules abundant; heavy radiolaria present though few.
3. Not transported a great distance nor by swift currents to the present position, as the diatoms, though somewhat broken by pressure, show no wear; also, as there is an absence of any appreciable quantity of sand, shells, clay, etc.
4. Not a complex of materials from different localities, as the diatoms, though abundant, are remarkably few in species, being chiefly two species of *Coscinodiscus*.
5. Slowly and evenly deposited in their present situation with regular fluctuations in quantity (seasonal?), resulting in the mass being formed in thin laminated plates, easily separable, but uniform in composition.

It looks as if my samples were laid down *in situ*, in some quiet, shallow marine bay, into which no considerable quantity of fresh-water drained.

Jordan and Gilbert's studies of the fossil fishes bear out still further the conclusion reached by Dr. Mann from the diatoms. A body of quiet bay waters swarmed with herring that sought out such an environment for the purpose of spawning. Following the herring, came certain species of larger fish as predators upon them. In pursuit of these came, in turn, various pinnipeds, whose remains are being studied by Dr. Remington Kellogg. Under such a set of conditions as these forms would indicate, the student of birds would expect to find just such forms as have thus far come to light. All of them, except one limicoline, are fish-eating birds.

The most abundant bird collected in these beds to date is a species of shearwater not generically distinguishable from the persisting genus *Puffinus*. Those present-day ornithologists who have seen the countless hordes of shearwaters crossing the mouth of Monterey Bay and who have noted the great degree of mortality that sometimes afflicts these visitors (the present writer counted 30 dead bodies on 100 paces of the beach near Lompoc) can readily picture the scene as it probably was in Miocene time.

## AGE OF THE FORMATION.

Concerning the age of the Lompoc diatom beds, the following quotation from a letter by Dr. Bruce L. Clark, of the University of California, is submitted:

"I have not done individual work on the beds at Lompoc but they are mapped, and apparently correctly so, as being part of what is generally known as the Monterey. The horizon which I refer to is the Temblor horizon, *Turritella ocoyana* zone. . . . . Certainly the beds could not be younger than Upper Miocene and not older than Middle Miocene—that is, from the invertebrate point of view. In that region the Fernando Pliocene rests unconformably upon the Miocene Shales."

## DESCRIPTION OF SPECIES.

### Puffinus diatomicus, n. sp.

(Plates 1, 2, and 7a.)

*Puffinus diatomicus*, new species. Type specimen No. 26541, Museum of Palaeontology, University of California; cotype No. 1, Stanford University.

As shown in plate 1, the type specimen includes the major portion of the skeleton in which a number of the more characteristic bones are well represented by imprints. The cotype includes only the left wing with the proximal portion of the humerus obscured by the superposed coracoid. The central part of the shaft is badly mutilated, but the specimen is of much interest because the position in which the humerus lay resulted in a perfect imprint of its distal end from directly in front. The peculiar ectocondylar process on this portion of the bone is very beautifully impressed upon the matrix.

In addition to the type and the cotype, there are two fairly complete specimens and a fragment that are referable to the same species. All five specimens correspond very closely in characters and in proportions of the parts which they display in common. The slight differences in recorded measurements are due largely to inability to obtain, within a millimeter or two, the exact contours of the several bones. When laid side by side, the specimens show a greater degree of homogeneity than the recorded dimensions would indicate.

*Description of the type specimen.*—The type slab is the most beautifully preserved of all the specimens of Lompoc birds thus far examined. The skeleton lies upon the left side. Around it, on the white background of the matrix, are dark markings that represent the remains of feathers, but they are too poorly preserved to be of more than general interest. The skull is shown in profile and displays almost a typical *Puffinus* physiognomy. The hook at the beak tip is set off less distinctly from the rest of the beak in the figure than is really true of the specimen, owing to the way that the matrix cleft at that point; the cleavage was not exactly on the median line in that region. The horny sheath seems not to have been preserved long enough to fix its impression upon the matrix.

The cranial portion of the skull, posterior to the orbit, is too poorly preserved to be of great value beyond giving an indication of the profile which seems to have been appreciably fuller in the frontal region than is the skull of modern shearwaters. Whether or not this might be due to post-mortem distortion, it is not possible to state.

The vertebrae of the neck are much displaced and poorly preserved, some of them having been entirely lost. The trunk portion of the specimen is little better than a confused jumble of superposed bones, though from this confusion there may be picked out some points of interest. The posterior border of the sternum shows two widely open notches, such as appear in the shearwaters and gulls. The axial profile and a portion of the base of one coracoid and the pygostyle are portrayed with fair distinctness and they bear out the general *Puffinus* impression.

The limb bones constitute the most valuable portion of the skeleton in determining the relationships of the species. The superior aspect of one humerus and the inferior aspect of the other are shown in really excellent fashion and these bones constitute the most characteristic features of the specimen. The straight, flat shaft, the abrupt enlargements at either end, and the contours of these terminal portions are decidedly *Puffinus* characters.

The posterior limb bones show a considerable degree either of natural robustness or of distortion by crushing. Particularly is this distortion seen in the femur, the tibiotarsus, and in the ulnar segment of the wing. The tarsometatarsus is not preserved in the type and is shown in one other specimen with such distortion as to yield only the total length as a character.

Crushing seems to have had no effect upon the wing bones in the cotype. Here, as in the type, the closest relationship seems to have been with the Recent *Puffinus opisthomelas*.

The following table of measurements is taken from the four specimens that offer sufficiently perfect parts. They indicate that the Miocene bird was slightly shorter of wing and longer of leg than the Recent species of nearest kin.

*Table of measurement of Puffinus diatomacus and P. opisthomelas.*

| | P. opisthomelas. | Type. | Cotype. | No. 2. | No. 3. |
|---|---|---|---|---|---|
| | *mm.* | *mm.* | *mm.* | *mm.* | *mm.* |
| Humerus, length | 86 | 80 | 84 | 82 | .......... |
| Ulna, length | 78 | 75 | 79 | 76 | .......... |
| Carpometacarpus | 45 | .......... | 46 | 45 | .......... |
| Phalangeal, first | 21 | .......... | 21 | 21 | .......... |
| Phalangeal, second | .......... | .......... | 21 | .......... | .......... |
| Femur, length | 31 | 30 | .......... | 33 | .......... |
| Tibiotarsus between articulations | 65 | 73 | 72 | .......... | .......... |
| Cnemial process | 15 | 14 | .......... | .......... | .......... |
| Tarsometatarsus | 45 | .......... | .......... | 53 | .......... |
| Foot, presumably middle toe | 42 | .......... | .......... | 53 | .......... |
| Coracoid, axial border | 27 | 27 | 27 | .......... | 26 |
| Coracoid, costal border | 34 | .......... | .......... | .......... | 32 |
| Sternum, breadth anteriorly | 33 | .......... | .......... | 30 | .......... |
| Skull, length over all | 86 | 90 | .......... | .......... | .......... |
| Scapula | 42 | .......... | 48 | .......... | .......... |

## Sula willetti, n. sp.[1]

(Plates 3 and 8.)

*Sula willetti*, n. sp. Type specimen No. 26542, Museum of Palaeontology, University of California. Miocene, Lompoc, California.

Approximately the size of *Sula piscator*, but with ratios of the limb segments different. The brachium is shorter than in *S. piscator* and the manus longer; the tibiotarsus is shorter and the tarsometatarsus is longer; the forehead is more concave.

The specimen on which this species is based is, in some respects, the most perfect of any of those from the Lompoc shale. The block of matrix containing it was cleft in such fashion that two slabs of about equal thickness resulted, one showing the right side and the other the left of the same individual. These two imprints supplement each other to a degree that displays the characters of certain parts in very accurate detail. The position of the skeleton is such that it is impossible to decipher the bones of the trunk with exception of one coracoid. The skull and the distal limb segments are, on the other hand, exceptionally well displayed.

*Skull.*—The skull, shown in profile, bears the typical sulid beak, devoid of anterior nares. The profiles of culmen and of mandible are essentially the same as those of *S. bassana*. There appears a slightly greater concavity of the frontal region, but this constitutes practically the only divergence of the fossil from the Recent species, so far as the skull characters are preserved to us.

*Coracoid.*—The coracoid in this group of birds is a very characteristic bone. The posterior border of its humeral articulation is very strongly accentuated, while the articulation with the sternum is quite short. This condition of affairs gives to the head of the coracoid an enlargement almost equal to the base of the bone. The Miocene slab shows this character with great distinctness.

*Pelvis.*—The pelvic bloc is decidedly like that of modern *Sula*, even to the presence of two pairs of ribs borne by the first and second vertebrae of the synsacrum. These ribs in the modern *Sula* extend beyond the margins of the innominatas as free ribs,

[1] This species is named in honor of George Willett, of the Cooper Ornithological Club, a close student of the Pacific coast sea birds.

although solidly anchylosed with the ventral surfaces of those bones. A corresponding set of ribs, likewise free at the ends, is easily discernible, in the fossil specimen. They are not found in the specimens of cormorants, pelicans, *Fregata*, or *Anhinga* that are available for examination. The general proportions of the pelvis, the position of the acetabulum, the very decided, sharp prominences on the posterodorsal aspects of the acetabula, the almost rectangular form of the postsacral half of the pelvis—all are decidedly sulid characters noticeable in the fossil specimen.

*Anterior limb.*—The minor characters of the wing bones are obscured by distortion and by superposition. The olecranon region of the ulna and the carpal end of the radius and the almost rod-like straightness of these bones are in close coincidence with the corresponding parts of the Recent sulids. As previously stated, and as inspection of the table of measurements will show, the lengths of the various segments differ from those of *S. piscator* in shortness of the brachium and antibrachium, and in greater length of the manus.

*Posterior limb.*—Approximate length is the only character of the femur to be relied upon, all others having been lost. In the tibiotarsus, we see the sulid characters in the short cnemial process which gives an effect of squareness to the bone proximally. The fibula remains distinct for a long distance down the shaft and is firmly attached at its distal end, thus helping to broaden the already stubby bone in the lower shaft region. The characters of the anterior face of the distal end are decidedly those of *Sula*. The tarsometatarsus, one of the most characteristic bones of the avian skeleton is fortunately shown from both anterior and posterior faces. Details are somewhat obscured, especially in the case of the anterior face, yet the sulid nature of the fossil is emphasized by this segment. The intercotylar prominence is well defined; the cotylar margins are much lower in front than in rear, showing thus a decided angle between the tarsal and the tibial segments of the limb. The anterior face of the bone has much the same degree of excavation and the delineation of the trochlea against the anterior aspect of the shaft is very sharp, as in Recent birds of the group. The outer toe is less elevated than in *Sula bassana* and is noticeably weaker, although the ratio of lengths of the several toes is such as to make up a typical steganopod foot.

*Relative lengths of toes in Sula willetti and in Sula bassana.*

| | S. willetti. | S. bassana. |
|---|---|---|
| Hind toe | 0.187 | 0.28 |
| Inner toe | .70 | .72 |
| Middle toe | 1.00 | 1.00 |
| Outer toe | 1.018 | 1.00 |

Altogether, the species under discussion displays a more or less typical sulid structure that does not diverge markedly from the surviving birds of the genus *Sula*, in so far as the skeleton yields results. Its chief interest lies in its proof of great longevity in those same characters. Of especial interest to the writer personally is the closure, so long ago, of the external nares. Why did nature rob this entire group of birds of their nostrils? They are practically gone in the tropic birds. If the group has survived the loss since Miocene time, they must not have found it a great deprivation.

FIG. 1.—*Sula willetti*, diagram of segments of foot.

*Approximate measurements of Sula willetti.*

| | mm. | | mm. |
|---|---|---|---|
| Skull, total length | 129 | Tarsometatarsus | 41 |
| Mandible | 114 | Hind toe | 14 |
| Humerus | 156 | Inner toe | 53 |
| Ulna | 147 | Middle toe | 74 |
| Carpometacarpus | 70 | Outer toe | 75.5 |
| 1st phalanx of manus | 37 | Coracoid, axial border | 45 |
| 2d phalanx of manus | 23 | Synsacrum | 70 |
| Femur | 52 | Pelvis, width across acetabular prominences | 32 |
| Tibiotarsus between articulations | 71 | | |

### Sula lompocana, n. sp.

(Plates 4, 7*b*, and 9.)

*Sula lompocana*, n. sp. Type specimen No. 26544, Museum of Palaeontology, University of California.

Approximately the size of *Sula bassana* but with longer wings and decidedly weaker pelvis.

The slab representing this species is one of the least perfect of the Lompoc bird specimens. Crushing has distorted the long bones considerably, while the pelvis and several of the vertebrae are the only portions of the axial skeleton preserved with any degree of completeness. The axial border of the right coracoid is present, but it is very poorly preserved. Such characters as are preserved are in complete accord in emphasizing the sulid nature of the specimen. The species is assigned to the genus *Sula* with a measure of reserve, although all the discernible characters are referable to that genus.

The specimen very closely approximates in size the Recent *Sula bassana* and, except for the divergence noted in the synopsis above, is much the same type of bird. The coracoid and the femur are equal in length in the two species. Unfortunately the hind limbs are not sufficiently well preserved to determine whether or not the suggestion of weakness made by the pelvis is borne out by the extremities.

The characters relating the fossil species to the genus *Sula* may be enumerated as follows: Humerus long and straight and very square-ended proximally, the topography both dorsally and ventrally at the proximal end being decidedly that of *Sula*. Coracoid with the long head, short shaft, and wide articulation with the sternum. Pelvis very decidedly sulid in its generally quadrangular shape with very marked supra-acetabular prominences. This combination of characters is not found in any other steganopod family known to the writer, and the weakened pelvis is the only character not in accord with the typical genus of the Sulidae. It is thought best to assign to the genus *Sula* despite this divergence.

*Table of measurements of Sula lompocana.*

| | mm. | | mm. |
|---|---|---|---|
| Humerus, total length | 245 | Femur, length | 69 |
| Humerus, transverse diameter of head | 28 | Pelvis, length of synsacrum | 103 |
| Coracoid, length axial border | 62 | Pelvis, width through acetabular prominences | 40 |
| Scapula, length | 109 | | |

### Miosula media, n. gen. and sp.

*Miosula media*, new genus and species. Type specimen No. 26543, Museum of Palaeontology, University of California. Miocene, Lompoc, California.

Resembles *Sula* in the characters of the tarsometatarsus but approaches the cormorants in having shorter wings and stouter feet than the gannets.

The specimen upon which this species is based is but very poorly preserved except for the tarsometatarsus. Both these bones are so placed as to show the anterior faces with little, if any, distortion. Flexible glue casts were very successfully taken and yield a quite accurate impression of the original bone. The anterior aspect of the

tibial condyles and the ventral face of the coracoid are made known in the same manner, but the wing bones, though present in the slab, are badly distorted by crushing.

The tarsometatarsus exhibits characters very closely resembling *Sula bassana*. There is the same cotylar pattern almost to exactness. The intercotylar mound is of the same low type. The anterior face of the shaft is excavated broadly and deeply. The trochlea of the inner toe is low and the inner profile of the bone swings markedly toward the sagittal plane, while the outer profile is more nearly straight. In fact, if these bones alone were preserved, the specimen would at once be assigned to the genus *Sula*. The assignment would also be supported by the coracoid and the distal end of the tibiotarsus. The latter part, however, approaches the cormorants (*Phalacrororax*) in some degree.

The great discrepancy lies in the ratio of parts. The coracoid indicates a bird with a body slightly larger than the gannet, *Sula bassana*, but the legs and feet are stouter while the wings are very much shorter and the humerus much less straight. The genus seems to occupy a position intermediate between the gannets and the cormorants. The gannets are strong fliers and less active divers; the cormorants are weak fliers but can cover great distances under water. The extinct *Miosula* must have occupied an intermediate position which renders its generic name doubly significant. The fact that *Sula willetti*, a member of a surviving genus, was living at the same time is of considerable interest. It suggests that *Sula* was a relatively young genus and that it has survived where *Miosula* dropped out as an older stage along the line of specialization of *Sula* toward greater powers of flight and away from a more generalized ancestral stock.

*Table of approximate measurements of Miosula media.*

| | mm. | | mm |
|---|---|---|---|
| Humerus, maximum length | 180 | 1st Phalanx of manus | 35 |
| Ulna | 140 | 2d Phalanx of manus | 37 |
| Carpometacarpus | 81 | Tarsometatarsus | 64 |

Fossil sulids have twice been recorded in previous years from North American strata. *Sula loxostyla* Cope, from the Miocene of Maryland, was based on a badly mutilated coracoid[1] which Shufeldt later[2] considered to be not determinable and certainly not *Sula*. In the same paper in which he reviews Cope's species *Sula loxostyla*, Shufeldt describes *Sula atlantica* from the Miocene of New Jersey and his figures of the single specimen, the coracoid, show the bird to have been undoubtedly very closely related to the modern gannets. The three Lompoc sulids thus add greatly to our knowledge of these birds in previous geologic times, not only by adding to the number and range of species but by furnishing more complete skeletons than have heretofore been known from the group.

### Cerorhinca dubia, n. sp.

*Cerorhinca dubia*, n. sp. Type specimen No. 26546, Museum of Palaeontology, University of California, Miocene, Lompoc, California.

Very close to *Cerorhinca monocerata* with longer tibiotarsus and shorter tarsometatarsus.

This species, referred with some hesitation to the genus *Cerorhinca*, is represented by a single specimen that is not so well preserved as some of the others of the collection. The tibiae and the tarsi are the only characteristic bones included upon the slab. The phalanages of both feet are crowded together and badly superposed. There are several of the long, slender posterior ribs indicated, but the remainder of the skeleton was lost in the quarrying operations.

The proportion of tibia to tarsus is quite close to that seen in *Cerorhinca monocerata* and the osteological characters, as displayed in the anterior surfaces of these two bones,

[1] E. D. Cope, Trans. Amer. Phylos. Soc., n. s., XIV, 1870, p. 236.
[2] R. W. Shufeldt, Trans. Conn. Acad. Arts and Sci., 1915, vol. 19, p. 62, foot note.

are practically identical with those of the Recent bird. The cnemial processes of the tibiae and the trochlear portions of the tarsi are obscured, but the few characters that are preserved are decidedly those of *Cerorhinca.* Comparison with the nearly related *Cepphus columba* shows the tarsus to be much shorter and stouter than in that species, the shaft at center being almost as broad as the transverse diameter of the head. This bone in the fossil specimen seems to have suffered very little crushing, a fact probably due to its very stocky proportions. The middle toe in *Cepphus* is but 25 per cent longer than the tarsus. In the fossil it is 50 per cent longer—a character allying it decidedly with *Cerorhinca.*

There thus appear no characters in this somewhat imperfect specimen that are at great variance with those of *Cerorhinca monocerata,* hence the lesser of two evils appears to the author to lie in assigning the species to an existing genus even though such assignment extend the age of the genus back to Miocene time. Two other genera, *Puffinus* and *Sula,* are thus extended without reservation in the present paper. There seems, then, no impropriety in considering the same to be true of the genus to which this less perfect specimen is assigned, recognizing always that, to the avian oesteologist, the genus appears in a somewhat different light from what it does to the ordinary ornithologist.

*Measurements of Cerorhinca dubia.*

| | *mm.* | Phalanges of middle toe: | *mm.* |
|---|---|---|---|
| Tibia without cnemial crest | 60 | No. 1 | 15 |
| Tarsus | 29 | 2 | 11.5 |
| Middle toe | 44 | 3 | 11.7 |
| | | 4 | 6 |

**Limosa vanrossemi, n. sp.**

(Plate 6.)

*Limosa vanrossemi,* n. sp.[1] Type specimen No. 26545, Museum of Palaeontology, University of California. Miocene of Lompoc, California.

Approximately the size of *Limosa fedoa* but with different ratio of lengths of the posterior limb segments. Femur equal; tibiotarsus shorter; tarsometatarsus longer.

The slab of the matrix bearing this specimen is one of the most beautiful in the Lompoc collection of birds. The colorings of both specimen and background are respectively quite uniform dark and light. The specimen is posed with very little distortion and the trunk, seen in profile, has the ribs with their uncinate processes very beautifully defined. The effect is of very great completeness and hence unquestioned identity. Unfortunately, however, superposition of parts and the crushing of long bones by pressure render the specimen less determinable than at first seems to be the case.

The entire skull is lacking. The posterior border of the sternum, much of the pelvis, and details of the coracoid, tibiae, and tarsi are obscured. The first glance shows it to be a member of the Scolopacidae with affinities very close to the Recent curlews and godwits. The relationship seems closest to the godwits and from the existing *Limosa fedoa* it shows but slight divergence. The wing segments are almost identical with those of the modern bird, but with the posterior limb the case is different. The femur is identical in length, the tibia is appreciably shorter, and the tarsus appreciably longer. The basal margin of the coracoid is too poorly preserved to be definitely located. The outline of the sternal keel is not exactly that of either the godwit or the curlew but it is nearer that of the curlew, although much variation of this character is to be noted among Recent individuals within a species.

[1] The specific name here proposed is in honor of Adriaan J. Van Rossem, an ornithologist of merit, whose efforts have greatly assisted the present writer in assembling much needed comparative material.

There is no discernible character in the specimen that would exclude it from the genus *Limosa* and its size and the ratios of the limb segments indicate a close approximation to *Limosa fedoa*. The differences pointed out above are sufficient to throw it into a distinct species, thus far unknown.

*Measurements of Limosa vanrossemi.*

| | *mm.* | | *mm.* |
|---|---|---|---|
| Length of humerus | 77 | Length of tibia | 86 |
| Length of ulna | 82 | Length of tarsus | 77 |
| Length of carpus | 41 | Length of middle toe | 35 |
| Length of femur | 40 | Depth of sternal carina | 24 |

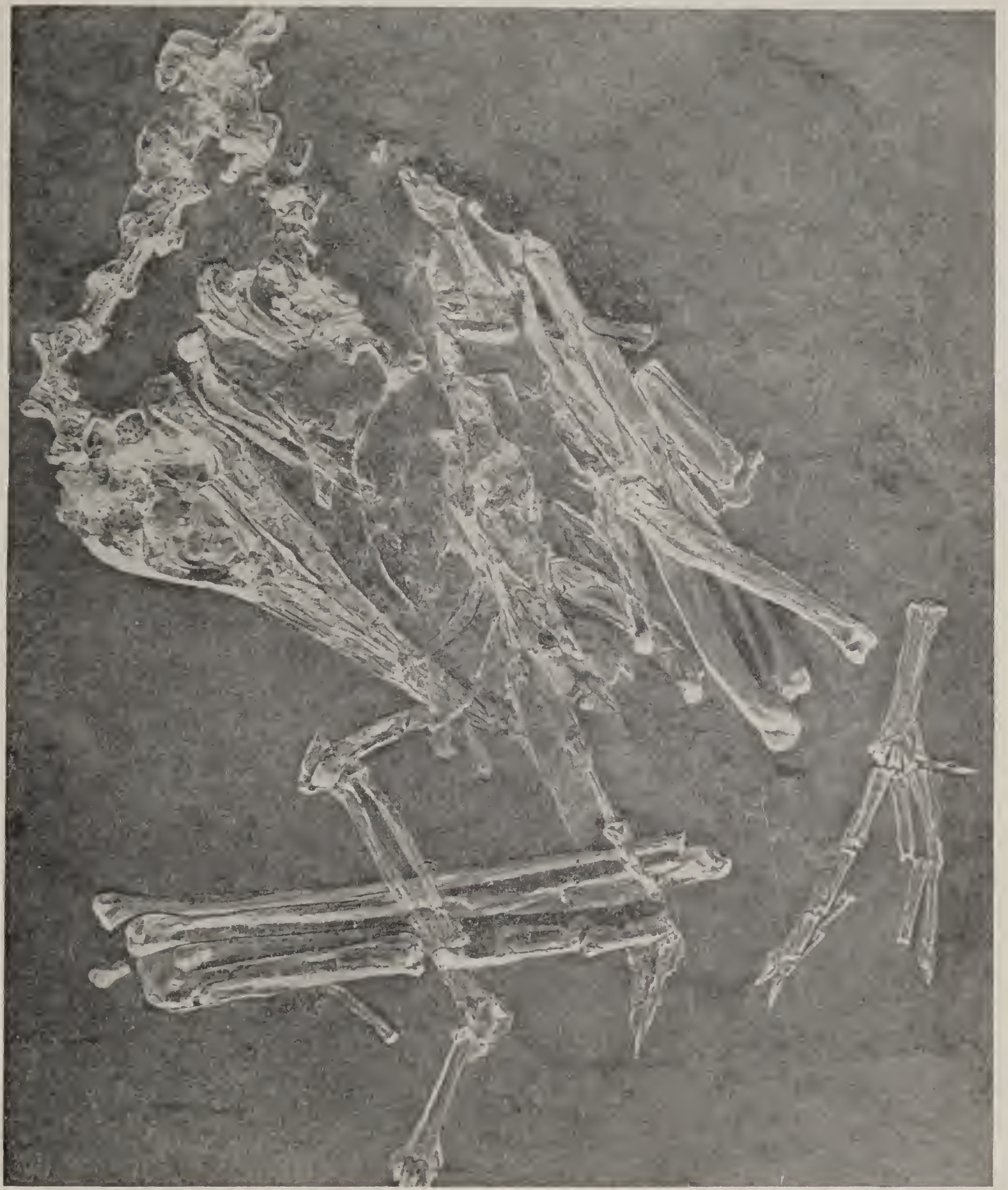
## SUMMARY.

Study of the bird remains supports the conclusions of Jordan and Gilbert as to conditions that prevailed during the accumulation of these beds. Six species of birds are represented, all new to science. One new genus is represented, a member of the Sulidae but less specialized for flight than the typical genus of that family. *Puffinus* and *Sula* are both genera that have been previously reported from strata of Miocene age. *Cerorhinca* and *Limosa* are new to American palaeontology. The close similarity of these Miocene forms to those of the same orders of birds living to-day is very well brought out by study of the Lompoc specimens.

*Puffinus diatomicus.* Type specimen No. 26541, Museum of Palaeontology, University of California. About one-half natural size.

*Puffinus diatomicus.* Cotype, Geological Collections of Stanford University. About natural size.

*Cerorhinca dubia.* Type specimen No. 26546. Museum of Palaeontology, University of California. About five-sixths natural size.

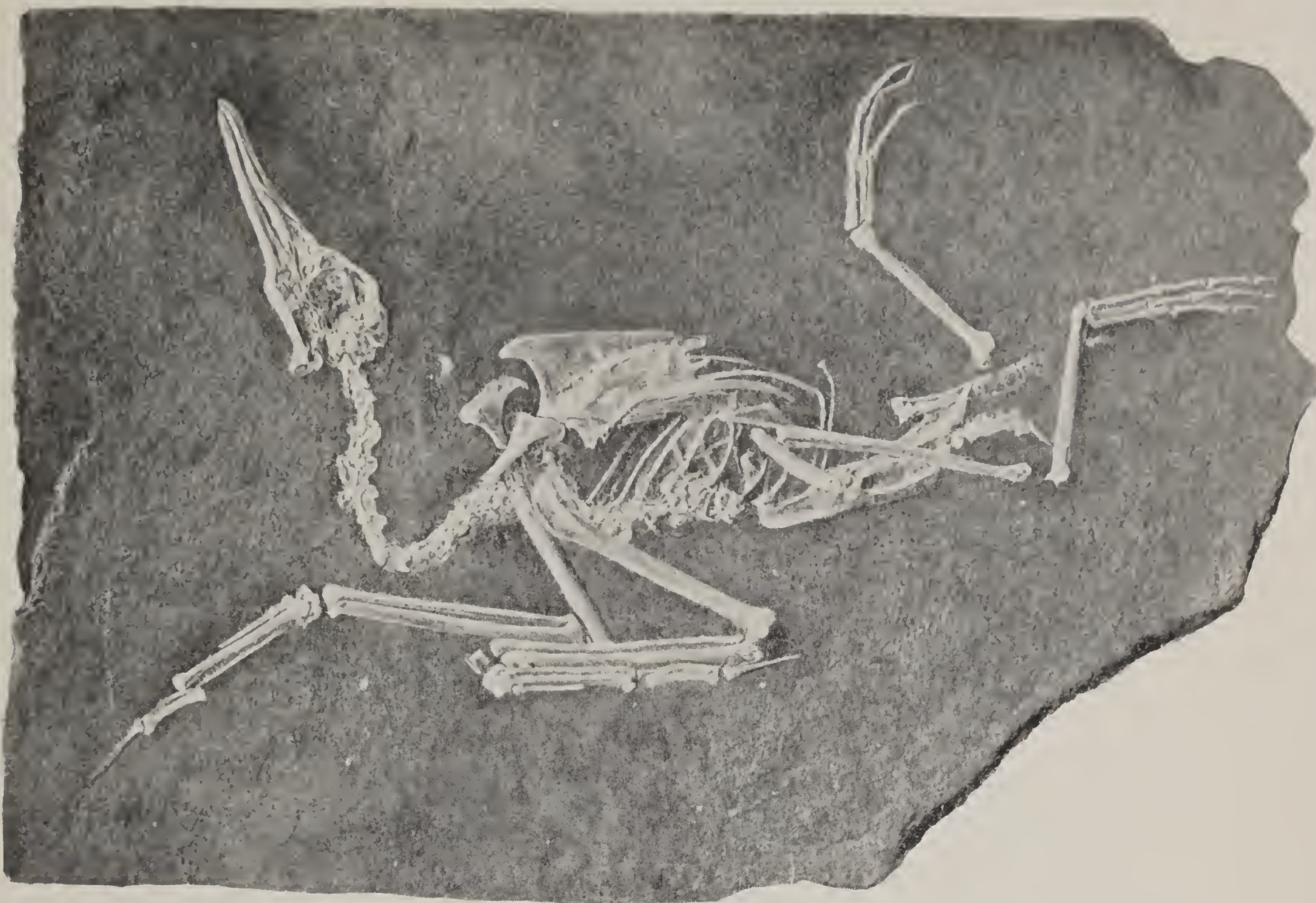


*Sula willetti.* Type specimen No. 26542, Museum of Palaeontology, University of California.
About one-half natural size.

*Sula lompocana.* Type specimen No. 26544, Museum of Palaeontology. University of California. About two-fifths natural size.

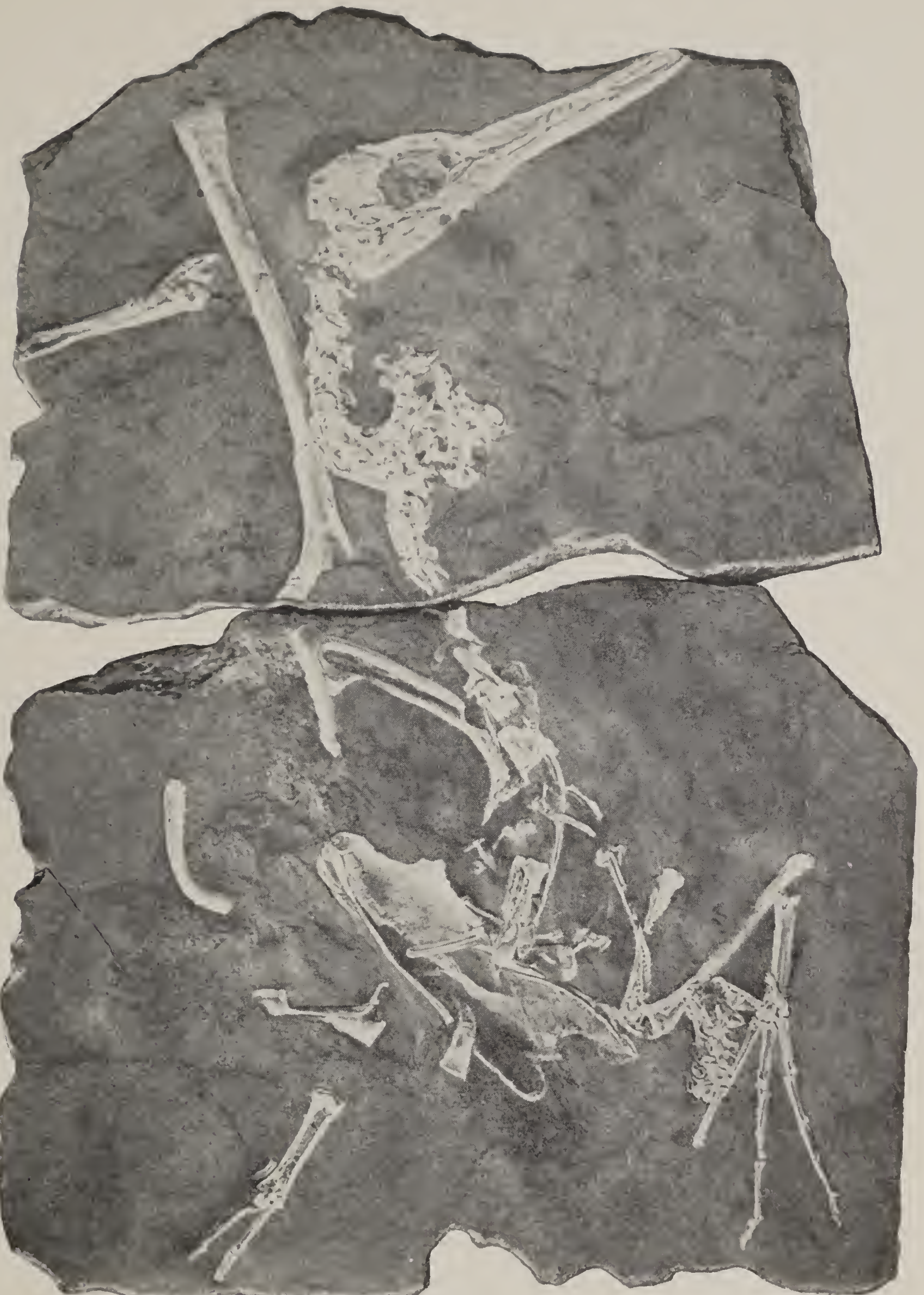
*Miosula media.* Type specimen No. 26543, Museum of Palaeontology, University of California. About two-fifths natural size.

*Limosa vanrossemi.* Type specimen No. 26545, Museum of Palaeontology, University of California. About one-half natural size.



A. *Puffinus diatomicus*, about four-tenths natural size. From a slab at the University of California, Southern Branch.

B. *Sula lompocana*, about natural size. From a slab at the University of California, Southern Branch.



*Sula willetti*, about eight-tenths natural size. From a slab at the University of California, Southern Branch.

*Sula lompocana,* approximately half-size. From a slab at the University of California, Southern Branch.

VII.

# RODENTS AND LAGOMORPHS OF THE RANCHO LA BREA DEPOSITS.

By LEE RAYMOND DICE.

With seventeen text-figures

# CONTENTS.

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# RODENTS AND LAGOMORPHS OF THE RANCHO LA BREA DEPOSITS.

By Lee Raymond Dice.

## INTRODUCTION.

The first collected remains of rodents and lagomorphs from the asphalt deposits of Rancho La Brea, Los Angeles County, California, were studied by Louise Kellogg.[1] From later collections a considerable amount of new material has been obtained, which has made it desirable to restudy the species.

All the specimens studied are in the Palaeontological Collections of the University of California. Much skeletal material is included in the collections, but attention has been directed entirely to the skulls, mandibles, and teeth, as taxonomic characters for identifying species and subspecies in these groups of animals have not yet been worked out for other parts of the skeleton. The drawings of the enamel patterns of the teeth have been made with the aid of a camera lucida on a microscope enlarging to 12 diameters; and each tooth was drawn separately from a point of view parallel to its dorso-ventral diameter.

Thanks are due Dr. J. C. Merriam for the opportunity to study the material and for criticism and advice during the progress of the work. Dr. Joseph Grinnell, of the California Museum of Vertebrate Zoology, kindly loaned many Recent specimens for comparison and furnished valuable information on the habitat preferences of the species in southern California. To Harry S. Swarth, of the Museum of Vertebrate Zoology, thanks are due for information concerning the condition and distribution of the present rodent habitats in the vicinity of Rancho La Brea.

## SIGNIFICANCE OF THE FAUNA.

The remains studied come from four stations or localities at Rancho La Brea. These localities have been described by Stoner,[2] and are numbered 1059, 2050, 2051, and 2052. Localities 1059, 2050, and 2051 are definitely Pleistocene in age and contain abundant remains of extinct genera and species, such as the ground-sloths, wolf (*Canis dirus*), sabre-tooth tiger (*Smilodon*), camel (*Camelops*), and horse

[1] Louise Kellogg, Pleistocene rodents of California, Univ. Calif. Publ. Bull. Dept. Geol., 7, 151–168 (1912).

[2] R. C. Stoner, Univ. Calif. Publ. Bull. Dept. Geol., 7, 387–396, pls. 16–21 (1913).

(*Equus occidentalis*). Localities 1059 and 2051 are in the same pit, representing two periods of work. Locality 2052 is more recent than the other deposits and may not be Pleistocene in age. One considerable collection of rodent material lost its label through an accident, and it is impossible to determine whether this collection is from locality 2051 or locality 2052. The bulk of the evidence seems to indicate that it is from locality 2051, and in the following accounts it has been mentioned as 2051(?).

No differences were found between the rodent and lagomorph faunas of the several fossil localities. This is not remarkable in view of the close similarity between the species represented by the fossils and the species of these groups now living in the Los Angeles region.

Table 1 is intended to facilitate the comparison of the fossil and living forms in the Los Angeles region. The list of species now living in the region has been prepared with the help of Dr. W. P. Taylor and includes the species known to be living near Los Angeles and probably living in the region of Rancho La Brea. No specimens of Recent mammals have been collected exactly at Rancho La Brea and this list may therefore be subject to slight modification.

TABLE 1.—*Comparison of fossil and recent rodents and lagomorphs of the Los Angeles region.*

| Species fossil at Rancho La Brea: | Species now living in Los Angeles region: |
|---|---|
| Onychomys torridus ramona. | Onychomys torridus ramona. |
| Reithrodontomys megalotis longicaudus. | Reithrodontomys megalotis longicaudus. |
| Peromyscus imperfectus. | |
| | Peromyscus maniculatus gambelii. |
| | Peromyscus californicus insignis. |
| | Peromyscus eremicus fraterculus. |
| Neotoma species. | Neotoma intermedia intermedia. |
| | Neotoma fusipes macrotis. |
| Microtus californicus neglectus. | Microtus californicus neglectus. |
| Thomomys bottae occipitalis. | Thomomys bottae pallescens. |
| | Perognathus panamintinus brevinasus. |
| Perognathus californicus californicus. | Perognathus californicus californicus. |
| Dipodomys agilis agilis. | Dipodomys agilis agilis. |
| Citellus beecheyi fisheri. | Citellus beecheyi fisheri. |
| Lepus californicus orthognathus. | Lepus californicus bennettii. |
| Sylvilagus audubonii pix. | Sylvilagus audubonii sanctidiegi. |
| Sylvilagus bachmani cinerascens. | Sylvilagus bachmani cinerascens. |

There are 11 genera and 21 species of rodents and lagomorphs represented in the asphalt deposits; of these, 1 species and 3 subspecies are considered to be peculiar to the deposits; 7 forms are represented also in the living fauna of southern California; and 1 form could not be specifically identified. All of the genera and many of the species now living in the vicinity of Los Angeles are present in the asphalt deposits. The few cases of differences between the fossil and living forms are considered to be only of subspecific value except in the case of *Peromyscus*.

In abundance, the remains of pocket-gophers far exceed all other species in the deposits. Next, in order of abundance, are the kan-

garoo-rats, pocket-mice, and cottontail rabbits. Of lesser abundance are the meadow-mice, deer-mice, and ground-squirrels; while the remains of harvest-mice, jack-rabbits, brush-rabbits, wood-rats, and grasshopper-mice are rare.

The occurrence of grasshopper-mice, pocket-mice, kangaroo-rats, black-tailed jack-rabbits, and brush-rabbits in the Rancho La Brea deposits indicates the close proximity of semi-arid conditions at the time the deposits were formed. On the other hand, the presence of harvest-mice, meadow-mice, and cottontails indicates the probable presence of moist soil conditions. From this evidence it appears likely that the habitats and climatic conditions near Los Angeles at the time of the formation of the deposits were very similar to those found in the neighborhood of Rancho La Brea at present: clumps of willows and brush or tall weeds along tiny streams in an open region mainly semi-arid in character. It is not necessary to assume from the evidence of these faunas that the climatic conditions of that time were exactly the same as now. The climate might have been slightly more moist than at present, though hardly more arid.

Whatever the cause of the extinction of the larger species of mammals inhabiting southern California in Pleistocene time, it could not have been due, seemingly, to any great variation in the climatic conditions of the region, for any considerable fluctuation in climatic conditions would surely have had some effect on the smaller mammalian fauna. Yet we find a very close similarity between the rodents and lagomorphs of the Rancho La Brea deposits and those living to-day in the Los Angeles region, and it seems impossible to escape the conclusion that there can not have been any considerable or widespread variation in the climate of the region between the Pleistocene and the present time.

## ANNOTATED LIST OF SPECIES.

### Onychomys torridus ramona Rhoads.

One jaw from the locality doubtfully 2051, another jaw from locality 2052.

These specimens show no characters by which they can be distinguished from the species of grasshopper-mouse now living in the Los Angeles region.

### Reithrodontomys megalotis longicaudus (Baird).

Three jaws from locality 2051, and three from locality 2051 (?).

No characters could be found which would serve to separate these remains from the living form of the region.

### Peromyscus imperfectus, new species.

*Peromyscus gambeli* (?) Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 166, 1912.

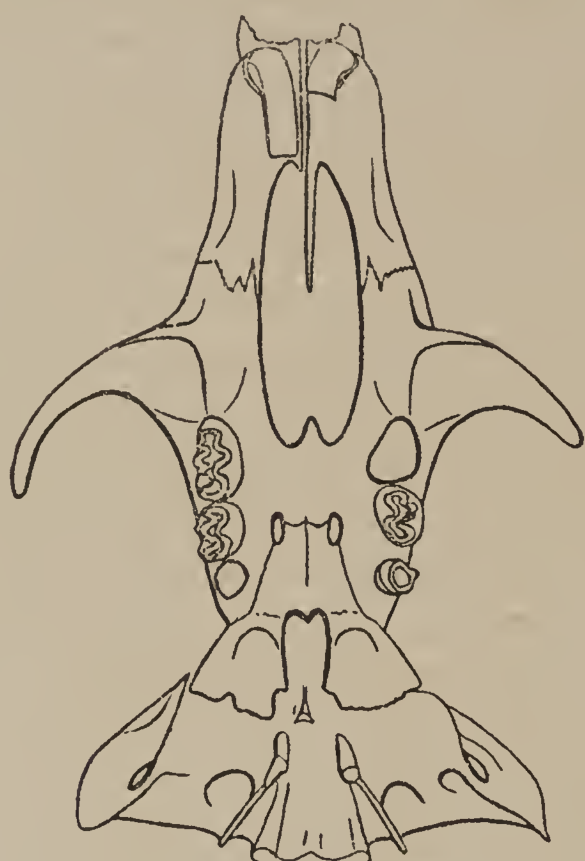
Type No. 21879 in the Palaeontological Collections of the University of California. A skull with right $M\underline{1}$ and $M\underline{2}$, and left $M\underline{2}$ and $M\underline{3}$ present; nasals, parietals, occipitals, bullae, and mastoids missing. From locality 20–N–1, 2051, Rancho La Brea deposits, Los Angeles County, California.

One jaw from locality 1059, 1 skull (type) and 5 jaws from 2051, 15 jaws from 2051 (?), and 7 jaws from 2052.

Size about that of *Peromyscus maniculatus gambelii*. Small accessory tubercules present on M$\underline{1}$ and M$\underline{2}$. Palatine slits proportionally longer and shelf of bony palate proportionally shorter than in the skulls of other species of the genus. The palatine slits are wide in front as in *P. m. gambelii* and not narrowed anteriorly as in *P. eremicus fraterculus* and in *P. e. crinitus*.

The presence of accessory tubercules on the molars indicates that this species should be placed in the subgenus *Peromyscus*. Its relationships to the other species in the subgenus can not be determined from the incomplete skull available for study.

1



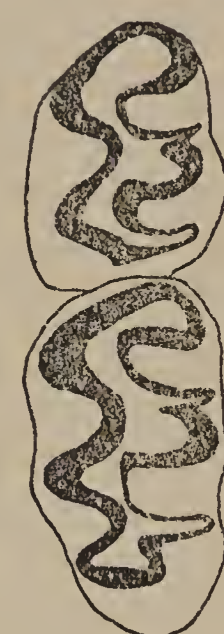


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FIG. 1.—*Peromyscus imperfectus*. Ventral view of skull, ×2. Type, U. C. Coll. Vert. Palaeon., No. 21879 /2051. Rancho La Brea deposits, California.

FIG. 2.—*Peromyscus imperfectus*. Right M$\underline{1}$ and M$\underline{2}$. ×8. Type, U. S. Coll. Vert. Palaeon., No. 21879 /2051. Rancho La Brea deposits, California.

TABLE 2.—*Measurements of type of Peromyscus imperfectus.*

| | *mm.* | | *mm.* |
|---|---|---|---|
| Interorbital constriction | 4.1 | Maxillary tooth row | 3.6 |
| Shelf of bony palate | 3.5 | Width of palate at M$\underline{3}$ | 2.2 |
| Palatine slits | 5.8 | Width of rostrum at anterior border of palatine slits | 3.7 |
| Diastema | 6.5 | | |

### Neotoma species.

One jaw from locality 2050, another jaw from 2051, and another from 2051(?).

A specimen from locality 10–D–13, 2050 retains the incisor, M$\overline{1}$, and M$\overline{2}$, though the hinder portion of the jaw is broken. From the enamel patterns of the molars it is possible to determine that this specimen does not belong to the subgenus *Teonoma*, but not possible to determine whether it belongs to the subgenus *Neotoma* or to *Homodontomys*. In size the specimens are small, but fall within the range of variation of *Neotoma i. intermedia* and of *N. fusipes macrotis*.

### Microtus californicus neglectus Kellogg.

*Microtus californicus* Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 166, 1912.

Three skulls and 8 jaws from locality 1059, 4 jaws from 2051, 6 skulls and 9 jaws from 2051(?), and 1 skull and 1 jaw from 2052.

On the character of the incisive foramina and the enamel patterns of the molars these specimens must be placed in the *M. californicus* group. In size and general proportions they are referable to the subspecies at present living in the region.

**Thomomys bottae occipitalis, new subspecies.**

*Thomomys bottae pallescens* Kellogg, Univ. Calif. Publ. Dept. Geol., vol. 7, 167, 1912.

Type. No. 21876 in the Palaeontological Collections of the University of California, from locality 20–N–1, 2051, Rancho La Brea deposits, Los Angeles County, California. The type is the nearly perfect skull of a fully grown and moderately old individual. The nasals are missing and the pterygoids are broken, though otherwise the specimen is in good condition.

Two skulls and 8 jaws from locality 1059, 2 skulls and 2 jaws from 2050, 21 skulls and 50 jaws from 2051, 64 skulls and 129 jaws from 2051(?), and 38 skulls and 100 jaws from 2052.

Skull similar to that of *Thomomys bottae bottae*, but the occipital slopes more strongly forward from the base and the condyles project more strongly to the rear.

In the *Thomomys bottae* group the slope of the occipital is subject to age, sex, and individual variation. In adults the forward slope is much stronger than in the young, and in males it is more pronounced than in females. However, in each of the Rancho La Brea specimens where the posterior part of the skull is preserved the forward slope of the occipital is stronger than in specimens of comparable age of any living member of the *bottae* group. In no Recent specimen examined is the forward slope of the occipital so strongly marked as in specimens of old individuals from Rancho La Brea.

TABLE 3.—*Thomomys bottae occipitalis in Rancho La Brea Deposits.*

| | Sp. No. 21876, locality No. 2051. | Sp. No. 21877, locality No. 2051. | Sp. No. 21878, locality No. 2052. |
|---|---|---|---|
| | *mm.* | *mm.* | *mm.* |
| Condyle to front of premaxilla | 45.0 | 42.3 | 43.7 |
| Zygomatic breadth | 28.9 | 26.6 | .............. |
| Height of cranium above front of palate | 16.2 | 16.0 | 16.8 |
| Interorbital breadth | 7.0 | 6.1 | 6.4 |
| Breadth of muzzle at front of maxillae | 8.9 | 8.2 | 8.5 |
| Breadth of muzzle at root of zygoma | 7.5 | 8.2 | 7.9 |
| Breadth of skull at post-glenoid notch | 17.7 | 17.2 | 18.8 |
| Upper molar series on alveoli | 9.0 | .............. | .............. |
| Diastema | 15.8 | 15.3 | 15.2 |

**Perognathus californicus californicus Merriam.**

Seven skulls and 21 jaws from locality 2051, 8 skulls and 41 jaws from 2051(?), 9 skulls and 7 jaws from 2052.

Remains of pocket mice are quite numerous in the tar deposits. All seem referable to the one species.

**Dipodomys agilis agilis (Gambel).**

*Perodipus agilis* Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 167, 1912.

One skull from locality 1059, 6 skulls and 10 jaws from 2051, 20 skulls and 57 jaws from 2051(?), 18 skulls and 24 jaws from 2052.

All the skulls have lost the bullae and mastoids, and for that reason their specific identification is difficult. However, all seem referable to the species now common along the coast of southern California.

**Citellus beecheyi fisheri (Merriam).**

*Citellus beecheyi captus* Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 164, 166, 1912.

Four skulls and 9 jaws from locality 1059; 3 jaws from 2050; 2 skulls and 6 jaws from 2051; 1 skull and 3 jaws from 2052.

The Rancho La Brea ground-squirrel was described by Miss Kellogg as a subspecies, *captus*, with the following most important characters: distance between the premaxillae

short, palate narrow anteriorly, bullae relatively long and narrow, lower tooth row long, the lower molar teeth heavy.

With the additional material now on hand from Rancho La Brea in comparison with a series of Recent specimens of *Citellus b. fisheri* from various parts of its range in California, it seems that all of the characters given for the fossil subspecies fall within the limits of variation of the living form (table 4). All the measurements included in Table 4 were taken by the author and were made between similar points so as to be comparable. In several cases the measurements of the type of *captus* given by Miss Kellogg could not be verified, perhaps because she used other points than those here used.

TABLE 4.—*Citellus beecheyi group.*

| | *C. b. captus* Rancho La Brea. | Average of | *C. b. fisheri* (10 adults) Recent. |
|---|---|---|---|
| | *mm.* | | *mm.* |
| Interorbital breadth | 13.9 (13.+ – 15.0) | 4 | 13.9 (13.0 – 15.0) |
| Width between premaxillae at posterior edge | 12.6 (11.0 – 13.5) | 4 | 12.4 (11.0 – 14.0) |
| Anterior width of palate at P$\underline{3}$ | 8.8 (8.3 – 9.3) | 4 | 9.1 (8.5 – 10.1) |
| Posterior width of palate, back of M$\underline{3}$ | 8.6 (8.2 – 9.0) | 4 | 8.5 (7.8 – 9.3) |
| Upper tooth row on alveoli | 11.8 (11.2 – 12.2) | 4 | 11.9 (11.1 – 12.6) |
| Antero-posterior diameter of auditory bullae | 13.8 (.... ....) | 1 | 12.7 (11.8 – 13.8) |
| Transverse diameter of auditory bullae | 10.9 (.... ....) | 1 | 11.4 (10.4 – 12.4) |
| Lower tooth row on alveoli | 11.9 (11.3 – 12.3) | 5 | 11.5 (11.0 – 12.2) |
| Antero-posterior diameter of— | | | |
| P$\overline{4}$ | 2.5 (2.2 – 2.7) | 4 | 2.3 (2.2 – 2.8) |
| M$\overline{1}$ | 2.6 (2.4 – 2.9) | 5 | 2.4 (2.3 – 2.7) |
| M$\overline{2}$ | 2.9 (2.8 – 3.2) | 5 | 2.6 (2.4 – 2.8) |
| M$\overline{3}$ | 3.2 (... ...) | 1 | 3.4 (3.1 – 3.7) |
| Transverse diameter of— | | | |
| P$\overline{4}$ | 2.5 (2.2 – 2.8) | 4 | 2 7 (2.2 – 3.0) |
| M$\overline{1}$ | 3.0 (2.9 – 3.2) | 5 | 3.1 (2.8 – 3.4) |
| M$\overline{2}$ | 3.2 (3.2 – 3.3) | 5 | 3.3 (3.1 – 3.7) |
| M$\overline{3}$ | 3.2 (... ...) | 1 | 3.2 (2.9 – 3.6) |

The skulls in this group of ground-squirrels are quite variable in shape and size. Until more material is available from the asphalt deposits or until the skull variations in the *Citellus beecheyi* group are more fully known, it seems advisable to refer the Rancho La Brea specimens to the living form.

### Lepus californicus orthognathus,[1] new subspecies.

Type No. 21866 in the Palaeontological Collections of the University of California, a mandible with the vertical ramus and angular process lacking, check teeth present except M$\overline{3}$. From locality 10–D–13, 2050, Rancho La Brea deposits, Los Angeles County, California.

One jaw from locality 1059, 1 skull and 2 jaws (one the type) from 2050, and 1 skull from 2051.

Anterior portion of the horizontal ramus of the mandible much more nearly straight than usual in the subgenus *Macrotolagus;* diastema longer and cheek teeth with an average less transverse diameter than in *Lepus californicus bennettii.*

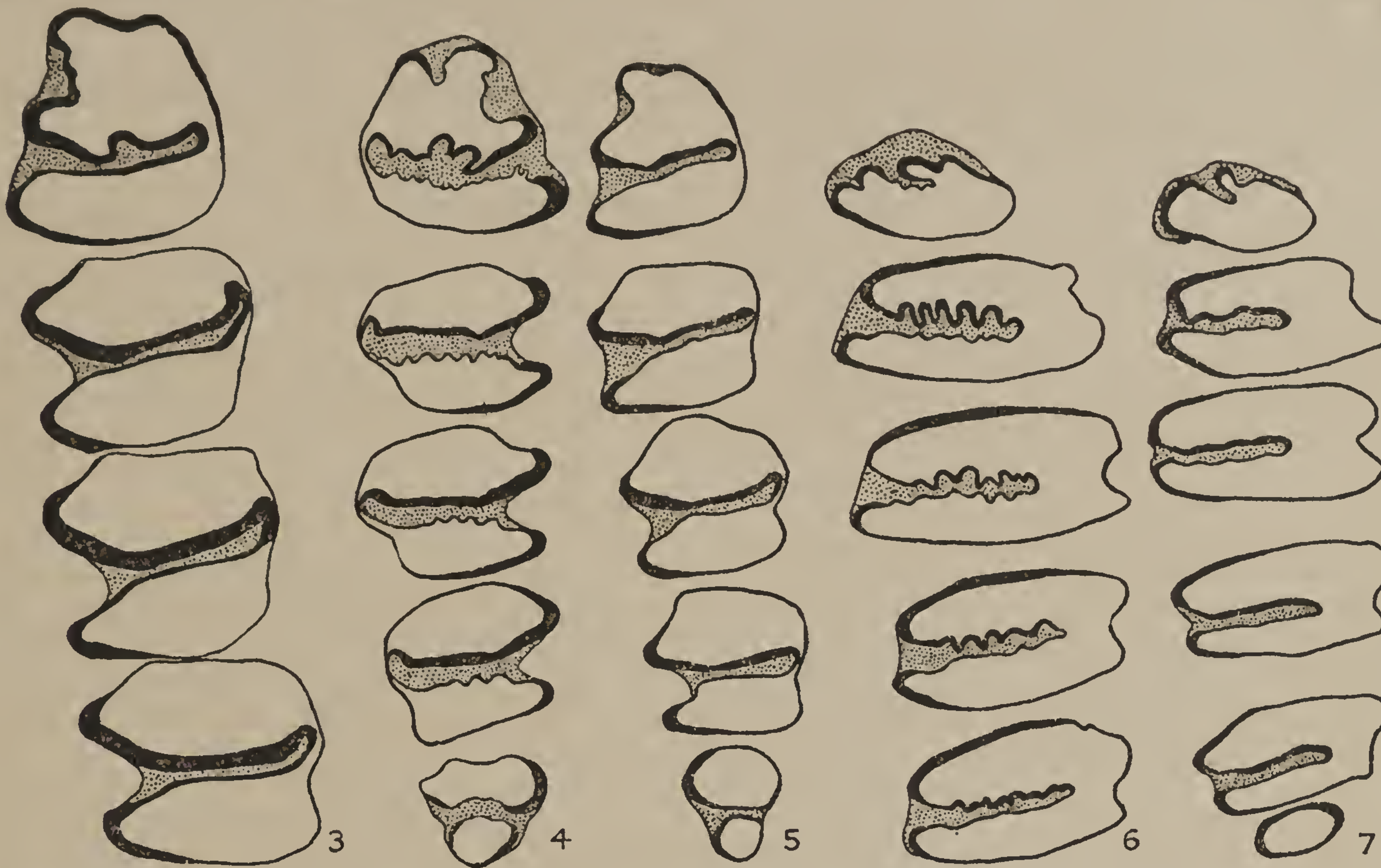
The jack-rabbit remains from Rancho La Brea evidently belong to the subgenus *Macrotolagus.* The skulls are not strongly arched as in the subgenus *Lepus,* and the postorbital processes join the skull, forming an inclosed foramen. The enamel patterns of the teeth also agree with those found in living members of the subgenus *Macrotolagus.* In general characters the remains show an evident relationship to the *Lepus californicus* group.

[1] ὀρθός, straight; γνάθος, jaw.

In living members of the subgenus *Macrotolagus* there is a pronounced upward bending of the anterior portion of the horizontal ramus of the mandible, while in the Rancho La Brea specimens this part of the ramus is nearly straight, or shows only a very slight upward curve.

In comparison with specimens of *Lepus c. bennettii* the fossil form has a distinctly longer diastema. However, of the fossil specimens only the type has the anterior portion of the jaw in good condition.

The folding of the enamel patterns of the molars seems to be on the average slightly less complex in the fossil than in the living form.



3 4 5 6 7

FIG. 3.—*Lepus californicus orthognathus.* Enamel patterns of left, lower molariform teeth ($M\bar{3}$ missing), ×3. Type, U. C. Coll. Vert. Palaeon., No. 21866/2050. Rancho La Brea deposits, California.

FIG. 4.—*Sylvilagus audubonii pix.* Enamel patterns of right, lower molariform teeth, ×3. Type, U. C. Coll. Vert. Palaeon., No. 21862/2051. Rancho La Brea deposits, California.

FIG. 5.—*Sylvilagus bachmani cinerascens.* Enamel patterns of left, lower molariform teeth, ×3. U. C. Coll. Vert. Palaeon., No. 21861/1059. Rancho La Brea deposits, California.

FIG. 6.—*Sylvilagus audubonii pix.* Enamel patterns of left, upper molariform teeth ($M\underline{3}$ missing), ×3. U. C. Coll. Vert. Palaeon., No. 11231/1059. Rancho La Brea deposits, California.

FIG. 7.—*Sylvilagus bachmani cinerascens.* Enamel patterns of left, upper molariform teeth, ×3. Mus. Vert. Zool., No. 3679, male. Recent, Escondido, California.

TABLE 5.—*Lepus californicus group.*

| | *L. c. orthognathus* Rancho La Brea. | Average of | *L. c. bennettii* (4 adults) San Diego region (Recent). |
|---|---|---|---|
| *Skull:* | *mm.* | | *mm.* |
| Least temporal breadth | 14.2 (14.0–14.5) | 2 | 12.2 (11.6–13.2) |
| Greatest temporal breadth | 31.4 (30.8–32.1) | 2 | 30.5 (29.1–31.3) |
| *Jaw:* | | | |
| Front of jaw to alveolus of $P\bar{3}$ | 23.2 (.... ....) | 1 | 19.9 (18.0–21.5) |
| Lower tooth row on alveoli | 16.3 (15.7–17.1) | 3 | 16.5 (15.8–17.0) |
| Trans, diam $P\bar{3}$ on face | 3.3 (3.1– 3.5) | 3 | 3.4 (3.0– 3.7) |
| $P\bar{4}$ | 3.4 (3.3– 3.4) | 3 | 3.8 (3.6– 4.0) |
| $M\bar{1}$ | 3.3 (3.2– 3.5) | 3 | 3.6 (3.4– 3.8) |
| $M\bar{2}$ | 3.2 (3.0– 3.3) | 3 | 3.6 (3.4– 3.8) |

### Sylvilagus audubonii pix,[1] new subspecies.

*Sylvilagus auduboni* Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 167, 1912.

Type, a complete right jaw with all teeth in place, No. 21862 in the Palaeontological Collection of the University of California. From locality 20–N–1, 2051, Rancho La Brea deposits, Los Angeles County, California.

Five skulls and 17 jaws from locality 1059, 2 skulls and 1 jaw from 2050, 2 skulls and 11 jaws from 2051, 5 skulls and 10 jaws from 2051(?), 5 skulls and 7 jaws from 2052.

Mandible averaging smaller than in *Sylvilagus a. audubonii*, the vertical ramus decidedly weaker; and the molariform teeth smaller.

The fossils measured for the table represent adults and are from localities undoubtedly Pleistocene (1059, 2050, and 2051).

Table 6.—*Sylvilagus audubonii group.*

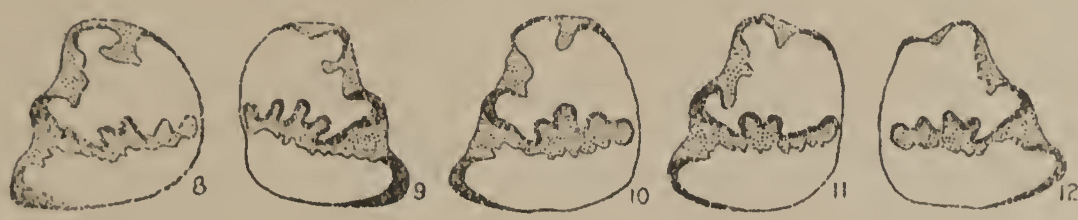
| | *S. a. pix* (Pleistocene) Rancho La Brea. | Average of | *S. a. sanctidiegi* (5 adults) San Diego region (Recent). | *S. a. audubonii* (3 adults) San Francisco region (Recent). |
|---|---|---|---|---|
| *Skull.* | *mm.* | | *mm.* | *mm.* |
| Width over zygomatic processes of maxillae | 29.9 (29.0–30.8) | 2 | 31.9 (30.0–33.5) | 32.4 (31.4–33.5) |
| Least temporal breadth | 12.5 (11.6–13.7) | 4 | 12.4 (11.8–12.9) | 12.4 (11.7–12.8) |
| Greatest temporal breadth | 26.9 (26.5–27.3) | 2 | 26.3 (25.4–26.9) | 27.0 (26.0–27.7) |
| Width of palate at P$\underline{2}$ | 9.2 (8.6– 9.8) | 2 | 8.6 (7.9– 9.3) | 8.8 (8.7– 8.9) |
| Upper tooth row on alveoli | 11.9 (11.0–12.5) | 3 | 12.8 (11.7–13.3) | 13.1 (12.3–13.9) |
| Trans. diam. P$\underline{2}$ on face | 2.7 (2.2– 3.0) | 4 | 3.0 (2.7– 3.6) | 2.8 (2.7– 3.0) |
| P$\underline{3}$ | 4.0 (3.4– 4.5) | 3 | 4.2 (3.8– 4.3) | 4.2 (4.0– 4.7) |
| P$\underline{4}$ | 3.8 (3.4– 4.3) | 4 | 4.1 (3.8– 4.3) | 4.0 (3.7– 4.4) |
| M$\underline{1}$ | 3.9 (3.4– 4.3) | 5 | 4.0 (3.5– 4.2) | 4.0 (3.9– 4.1) |
| M$\underline{2}$ | 3.6 (3.4– 3.8) | 3 | 3.7 (3.2– 3.9) | 3.6 (3.4– 3.8) |
| *Jaw.* | | | | |
| Front of jaw to alveolus P$\overline{3}$ | 14.2 (13.0–15.7) | 12 | 15.9 (15.2–16.9) | 15.9 (15.3–16.5) |
| Greatest width of vertical ramus | 19.0 (17.8–19.5) | 4 | 20.5 (19.7–21.6) | 21.2 (21.0–21.5) |
| Postangular process to preangular process | 19.8 (18.1–20.5) | 4 | 22.3 (20.7–23.6) | 22.4 (21.6–23.2) |
| Postangular process to front of jaw | 46.0 (44.5–47.5) | 4 | 49.6 (48.1–51.7) | 50.4 (49.2–51.9) |
| Thickness of mandible at M$\overline{1}$ | 4.0 (3.8– 4.4) | 15 | 4.3 (4.0– 4.7) | 4.3 (3.8– 4.5) |
| Lower tooth row on alveoli | 12.6 (12.0–13.6) | 13 | 12.9 (12.4–13.7) | 13.4 (12.6–14.4) |
| Trans. diam. P$\overline{3}$ on face | 2.7 (2.5– 2.9) | 9 | 2.7 (2.5– 2.8) | 2.6 (2.4– 2.8) |
| P$\overline{4}$ | 2.6 (2.5– 2.9) | 15 | 2.8 (2.7– 3.0) | 2.8 (2.6– 3.1) |
| M$\overline{1}$ | 2.6 (2.3– 2.9) | 15 | 2.8 (2.6– 3.1) | 2.7 (2.5– 3.0) |
| M$\overline{2}$ | 2.5 (2.3– 2.6) | 14 | 2.7 (2.5– 2.9) | 2.8 (2.6– 2.9) |
| M$\overline{3}$ | 1.6 (1.4– 1.7) | 6 | 1.6 (1.5– 1.7) | 1.6 (1.5– 1.7) |

Adult specimens of the *Sylvilagus audubonii* group can usually be distinguished from adult specimens of the *S. bachmani* group by the measurements, as the cottontail is distinctly larger than the brush-rabbit. The folding of the enamel on certain teeth is also important in separating these groups. The teeth which are particularly useful for this purpose are the third lower premolars and the first and second upper molars.

The enamel folding on the large re-entrant angle of P$\overline{3}$ is usually quite simple in the *S. bachmani* group. The enamel of the anterior half of this angle at about the middle always shows a strong backwardly directed point, but is normally not further folded (fig. 5). A single specimen of Recent *S. b. cinerascens* was found to show a simple

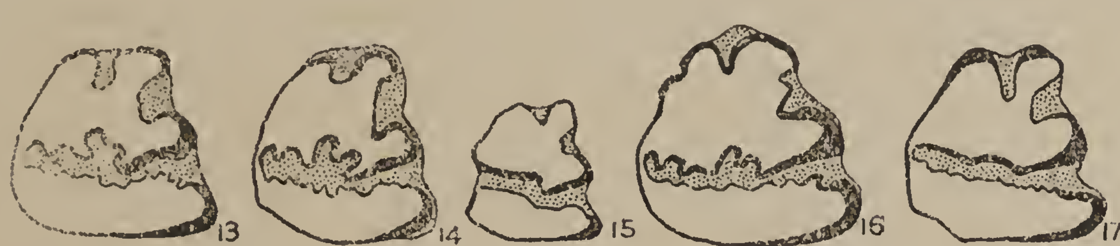
[1] *pix*: Lat., tar, pitch.

crenation on the inner part of this angle. In the *S. audubonii* group the anterior half of the main re-entrant angle of this tooth, P$\overline{3}$, shows normally two forwardly projecting loops, and interior to these the enamel is more or less wavy or crenated (fig. 4.).



FIGS. 8–12.—*Sylvilagus audubonii pix.* Enamel patterns of P$\overline{3}$, ×3. Rancho La Brea. U. C. Coll. Vert. Palaeon. Fig. 8, No. 21873/1059; fig. 9, No. 17270/1059; fig. 10, No. 21865/2051; fig. 1 1, No. 19248/1059; fig.12, No. 21880/2051.

In one Recent specimen (fig. 17) of *S. a. sanctidiegi* from the Tijuana River, southern California, the pattern of the principal fold of P$\overline{3}$ is almost the same as the normal pattern in the *bachmani* group. Out of about 50 specimens of adult *audubonii* examined this was the only one in which the pattern was simplified to any considerable degree. Very young specimens of *audubonii* also show a simple enamel pattern (fig. 15).



*Sylvilagus audubonii* group. Mus. Vert. Zool. Enamel patterns of right P$\overline{3}$, ×3. Recent.
FIG. 13.—*S. audubonii.* No. 18440, male, Walnut Creek, California.
FIG. 14.—*S. a. sanctidiegi.* No. 7567, male, Warner Pass, San Diego County, California.
FIG. 15.—*S. a. sanctidiegi.* No. 3770. male. juvenile. San Diego, California.
FIG. 16.—*S. a. sanctidiegi.* No. 3680, female, Escondido, California.
FIG. 17.—*S. a. sanctidiegi.* No. 3232, male, Tijuana River, San Diego County, California.

The enamel of the anterior edge of the re-entrant angles of the first and second upper molars seems never to be more than slightly wavy in the *S. bachmani* group, and is usually a nearly straight line (fig. 7). Of 13 adult specimens of Recent *S. a. sanctidiegi* from Southern California examined, the anterior edge of the enamel in the re-entrant angle of M$\underline{1}$ was crenated in every case, and in 8 of the specimens M$\underline{2}$ was in the same condition (fig. 6), while in the other 5 specimens this fold in M$\underline{2}$ was only slightly wavy.

The folding of the enamel on the teeth seems to be slightly more simple in the fossil than in the living forms of the *S. audubonii* group. However, one Recent specimen of *sanctidiegi* from the Tijuana River, California (fig. 17), has a simpler enamel pattern than any of the fossil specimens.

In the external characters of relative length of legs and ears the *Sylvilagus bachmani* group is less specialized than the *S. audubonii* group. The more simple enamel patterns in the *bachmani* group also indicate it as being the more primitive. This is further substantiated by the fact that the enamel pattern in young *audubonii* is like that of adult *bachmani*. From this evidence it may be assumed that the *bachmani* group represents a type similar to the probable ancestors of the *audubonii* group.

### Sylvilagus bachmani cinerascens (Allen).

*Sylvilagus bachmani cinerascens* Kellogg, Univ. Calif. Publ. Bull. Dept. Geol., vol. 7, 168, 1912.

Three jaws from locality 1059, one jaw from 2051(?) and one jaw from 2052.

One specimen from locality 1059 represents an adult and has all the cheek teeth in place. All the other specimens are badly broken or are from young individuals. On the characters of the enamel pattern the adult specimen must be placed in the *S. bachmani* group. The enamel folds of the teeth seem a little more rounded than in any modern member of the group, but this character is too variable to draw any conclusion from a single specimen. In measurements the specimen falls within the limits of variation of *S. b. cinerascens.*